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Created in 1849, the United States Department of the Interior—a department of conservation—is concerned with the management, conservation, and development of the Nation's water, fish, wildlife, mineral, forest, and park and recreational resources. It also has major responsibilities for Indian and Territorial affairs.

As the Nation's principal conservation agency, the Department works to assure that nonrenewable resources are developed and used wisely, that park and recreational resources are conserved for the future, and that renewable resources make their full contribution to the progress, prosperity, and security of the United States—now and in the future.

PREFACE

This is a revision of the first definitive handbook on marine decapod crustaceans of southeastern North America by Hay and Shore (1918).

The junior author, Clarence A. Shore (1873-1933), conceived the idea of the handbook while teaching in the medical school of the University of North Carolina at Chapel Hill. Shore entered the university in 1897, majored in biology, and earned the B.S. degree in 1901 and the M.S. in 1902. He spent several summers at the U.S. Bureau of Fisheries Marine Laboratory at Beaufort, N.C., where he developed an interest in taxonomy and ecology of crustaceans. In 1904 Shore began 3 years of study compiling descriptions and photographs of most of the decapod crustaceans known to occur in the region. He did not complete the work, however, for he left the field of marine biology to enter the field of medicine (Cooper, 1933, 1940; Wilson, 1933).

William Perry Hay (1871-1947), who graduated from Butler University in 1891, taught from

1892 to 1934 in schools and colleges in the Washington, D.C., area. He had a great interest in natural history, especially herpetology and carcinology, and published a number of papers in both fields (Needham, 1947). Hay took up Shore's uncompleted project in 1912, but found so much new data available that the original had to be revised. Thus the work was published 14 years after it was initiated.

The introduction to that book included a history of the project, a review of earlier work in the region, statements on affinities of the fauna, some ecological remarks, a few comments on arrangements of the hierarchy, and acknowledgments. Since 1918 knowledge has increased. Taxonomists have changed names and the faunal list has been expanded, although certain groups that Hay and Shore treated have been deleted in this revision. For these reasons, the general introduction which follows is a combination of those authors' comments and my own.

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MARINE DECAPOD CRUSTACEANS OF THE CAROLINAS

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INTRODUCTION

Knowledge of the crustacean fauna of the Carolinas has grown slowly over many decades. Early in the last century, Thomas Say described species from the Carolinas, and in the middle 1800's Professor L. R. Gibbes, who maintained a private collection in Charleston, S.C., described species from the Carolinas. William Stimpson (1860b), who visited Beaufort, N.C., in company with T. N. Gill, gave a list of 38 species of decapod crustaceans which he collected there. Elliott Coues (1871), at that time an Army surgeon stationed at Fort Macon, N.C., recorded 27 species of decapods from the Beaufort area, 8 of which were additions to Stimpson's list. Seven years later, Coues and Yarrow (1878) gave a list of six species, two of which had not appeared previously. An appendix to the same paper by J. S. Kingsley included 51 species from the Beaufort area, and 3 of these were additions to the fauna. A year later, Kingsley (1879) contributed eight more new records.

The collection which was the subject of Kingsley's report had been made by Professor H. E. Webster, of Union College. It was later transferred, in part at least, to the U.S. National Museum, and supplied the types of *Lepidopa websteri* Benedict and *Pinnixa cristata* Rathbun, both collected near Beaufort, N.C.

Professor W. K. Brooks and his students, of the Johns Hopkins University, studied crustaceans at Beaufort at intervals from 1880 to 1903. They

contributed information on habits and development, but only one or two new species were added to the faunal list.

Shore's manuscript included 87 species, but he omitted 8 which had been listed by the writers already mentioned. He had added 33 species, making a total of 95 species for the region.

Following this, exploratory work on offshore fishing banks by the *Fish Hawk* in the summers of 1914 and 1915, energetic shore and shallow-water collecting by parties from the Bureau of Fisheries laboratory at Beaufort, and inclusion of freshwater species from the region, enabled Hay to add 57 species to Shore's list. These, plus description of a new species by Rathbun, brought the total number known from Beaufort, N.C., in 1918 to 153 species.

The authors pointed out that some of these species had not yet been reported from the area, though from distribution elsewhere they might be expected. Also, some of the species were considered more properly to be deep-sea forms, rather than strictly members of the Beaufort fauna, although they had been found on the continental shelf not far distant.

In the year the handbook appeared, Mary J. Rathbun brought out the first in a series of four monographs on recent crabs of the Western Hemisphere, and, thus, began a new advance in knowledge of Carolinian crustaceans, later furthered by major revisions of the Penaeidae by Burkenroad, revisions of Hippolytidae, Palaemonidae and Scyllaridae by Holthuis, Galatheididae by

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Chace, Paguridae by Wass, Thalassinidea by de Man, Oxyrhyncha by Garth, and the Porcellanidae by Haig. Schmitt's treatment of the Macrura and Anomura of the Puerto Rican area, as well as his contributions on the Hippidae and the genera *Callianassa* and *Upogebia*, and Ver-rill's completion of the work on Bermudan decapods added breadth to knowledge of distribution as well as taxonomic stability. Closer at hand, the studies of Lunz in South Carolina yielded similar results. To this list of scholars could be added the names of Borradaile, Glassell, and Provenzano, who described new forms from the Carolinian province. The works of these and other authors are given in detail in the text to follow.

Apart from these primarily systematic studies, a growing number of ecological studies have been published during the past 45 years. Such results are not usually cited in systematic handbooks, but because this one is directed primarily to students and ecologists who are often newcomers to the area, brief summaries have been attempted. The review of literature, though not complete, is exhaustive enough to lead to most of the published material.

Actually, few species have been studied in detail. Of these, almost all are littoral species easily accessible to the investigator by virtue of their abundant numbers and ecological niches. Beyond this, a few species of commercial value such as *Callinectes sapidus* and *Penaeus* spp. have been studied in detail. It is fair to say that ecological studies are scarcely started.

SYSTEMATIC DISCUSSION

This is a review of published material. Arrangement of families and genera follows that adopted by the most recent reviser of each group. Important diagnostic characters of families and genera have been incorporated in keys and are often repeated, in part, in species descriptions. Brief diagnoses of families are included to aid in identification. Diagnoses of genera are not included, with some exceptions, for these exist in the literature. Such treatment leads to repetition but gives more complete descriptive accounts for individual species.

The general key to suborders, sections, superfamilies, and families serves as a rough index, and an attempt has been made to arrange it

"phylogenetically". Other keys to subfamilies, genera, and species are either combined or separate depending on number of genera or species involved, and these keys are scattered throughout the text.

There is a tendency in carcinology to assume a specialized background on the part of readers, and beginners may find themselves troubled with terms. A number of monographs have included introductory glossaries and figures with detailed labeling as aids, but these are not always adequate because terminology in various suborders and sections lacks consistency.

An illustration of inconsistency follows: Among shrimps, the pereopods are often called the first, second, third, fourth, and fifth walking legs. Among crabs, the tendency is to call the first pereopods, chelipeds, because they are almost invariably larger than the remaining legs and are the only chelate pair (except in anomuran and some dromiid crabs). The remaining pereopods are then termed the first, second, third, and fourth walking legs. This inconsistency seems firmly entrenched and it is based on functional morphology, the shrimps tending to have five pairs of legs functionally adapted to walking, but most crabs only four. Because many shrimps do not walk, legs in this group herein have been called "legs," the term "walking legs" being reserved for crabs. Hopefully, the use of explanatory figures adapted from existing works, together with the glossary, will resolve most of such difficulties.

In the species accounts, no attempt has been made to include complete synonymies. A great deal of spadework by recent specialists has made abbreviation of synonymies desirable and practical; therefore, most are restricted to citation of original description, Hay and Shore (where applicable), and work of the most recent reviser.

Many descriptions which Hay and Shore wrote have been paraphrased, and many measurements, descriptions of color, and ecological notes have been included essentially unchanged. When available, more recent information has been used, and for this I have depended heavily on Rathbun (1918b, 1925, 1930a, 1937), Schmitt (1935a), and Holthuis (1951a, 1952, 1959) for key characters, color notes, and depth and latitudinal ranges. For these works, specific citations in the text have often been excluded for the sake of brevity.

ZOOGEOGRAPHIC CONSIDERATIONS

Though the original title implied a local list, the handbook included an assemblage that is quite widespread. Hay and Shore justly termed it a virtual descriptive list of decapod crustaceans of the Middle Atlantic coast, in large measure filling but continuing in part from northwestern Florida the gap between various lists of New England, New York, and New Jersey crustaceans, and the Puerto Rican list (Rathbun, 1901). The assemblage treated, both by Hay and Shore (in the original) and this revised version, has a latitudinal range extending primarily from Cape Hatteras, N.C., to northeastern Florida (fig. 1), to Texas; it is encompassed in a more generalized assemblage sometimes recognized as the Carolinian province (Hedgpeth, 1953). Primarily Antillean in its affinities, the Carolinian province is distinct from the Virginian province to the north and this fact has been emphasized by numerous authors.

Bathymetric limits included in this revised handbook are altered somewhat from the original. Species which occur from the heads of estuaries to the 100-fathom contour are included. Fresh-water decapods, included in the original, have been excluded because they never occur in the marine environment. Species that occur only beyond the 100-fathom line more properly belong to a deep-sea fauna that ranges far beyond the Carolinian province, and are not included.

Arbitrary limits are difficult to establish. Judgments undoubtedly will differ as to what is extralimital and what is not. For some species with uncertain distributional limits, a list of extralimital species has been included.

An analysis of the decapod crustacean element in the Carolinian fauna is given by family in table 1. Here, categories chosen for limits in geographic range are used broadly, especially at their southern extremities. For economy of space, the term "South America" can mean either the northern or southern Atlantic shores of the continent, but details are given in the species accounts. Our interest here centers primarily on the eastern coast of North America, and on natural boundaries or barriers that exist on this stretch of coast.

It is apparent that a small number (6.8 percent) of Carolinian decapods are northern in affinity, extending to southern Florida in one case (*Cancer*

borealis). To this group, Cape Cod is no barrier, but to another group (12.7 percent) it is a barrier to northward extension into upper New England and the Maritime Provinces of Canada.

Totals are given for species extending northward to the Middle Atlantic States (9.1 percent). Many of these records are for accidental or seasonal occurrence; *i.e.*, species whose northern limits of range might well be set at Cape Hatteras. But there are other species in the group which must be permanent residents in those latitudes and are not dependent on annual repopulation from breeding stock to the south.

Cape Hatteras is a barrier to northward distribution of shallow-water forms. Here, warm water of the Gulf Stream meets the cold Labrador Current to be deflected seaward (Hutchins, 1947), and 27.7 percent of the decapods are apparently unable to bridge the narrow transition zone to colder water.

Cape Lookout, surprisingly, seems to be a greater barrier to northward extension of range among Antillean species (31.4 percent) than Cape Hatteras. This barrier may be real, or it may be that faunal limits fluctuate between these capes as a consequence of natural events. More likely is the fact that far more collecting has been done near Cape Lookout than at Cape Hatteras because of the nearness of marine laboratories to the former.

Species showing distributions reaching northward only to Charleston, S.C., (4.5 percent) are probably southern species with accidental records at that latitude, for there is no apparent barrier to dispersal in that area. Eastern and western Atlantic forms are equally small in number (4.5 percent).

Cosmopolitan species (1.8 percent) are few, as are endemic species (1.4 percent).

Aside from the above patterns of distribution, a number of species ranging along the Atlantic coast and the Gulf coast to Texas have a disjunct distribution in peninsular Florida. The number of these species is conservatively estimated, from literature records, at 10 percent of the total. This type of distribution, discussed at length by Hedgpeth (1953), shows a fairly recent separation of Gulf elements from the Atlantic portion of the species by emergence of peninsular Florida, but with the two areas being climatically equivalent



FIGURE 1.—Area of western North Atlantic Ocean, including portions of eastern North America, Middle America, and northern South America, covering centers of distribution for most species treated in this handbook.

(Hutchins, 1947). It is also clear, from families represented in this group, that many are relatively sedentary, at least as adults.

MATERIALS STUDIED

Materials studied at the U.S. National Museum (USNM) include recent records resulting from exploratory work by the vessels *Pelican*, *Albatross III*, *Combat*, *Oregon*, and *Silver Bay*, as well as records of collections by private individuals. Specimens studied were from the USNM, the Charleston Museum, Charleston, and Bears Bluff Laboratories, Wadmalaw Island, S.C., The University of North Carolina Institute of Fisheries Research (IFR), and various collections provided by Duke University Marine Laboratory and the U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C. Remnants of Hay and Shore's collections were also examined and are now housed at the IFR.

MEASUREMENTS

Measurements for individuals considered adult are either from the literature or from specimens examined. Sizes recorded usually represent the maximum. Width of the brachyuran carapace is the width including lateral spines. Length of shrimps includes the rostrum.

EXTRALIMITAL AND INDETERMINATE SPECIES

The following list includes species having doubtful position in the Carolinian fauna. Some range primarily in deep water, occurring incidentally on the Continental Shelf. Others have a range limited to shallow waters distant from the Carolinas. Some are included because Hay and Shore mentioned them, and the remainder have a doubtful taxonomic status.

Penaeopsis megalops (Smith). North Carolina, through Gulf of Mexico to Surinam; 150–200+ fathoms.

Sicyonia sp. (Lunz, 1945). A distinct specimen from Beaufort River, near Parris Island, S.C., has been described but not named (Charleston Museum No. 35.131.5(a)).

Hippolyte coerulescens (Fabr.). Central Atlantic Ocean, Bermuda, North Carolina to

Florida, Azores, Canary and Cape Verde Islands, Gulf of Guinea and S. Angola, doubtful from Cape Horn region (Sivertsen and Holthuis, 1956). A single mutilated male from Sneads Ferry, N.C., is in the U.S. National Museum.

Homarus americanus H. Milne Edwards. Labrador to North Carolina; shallow water to 100+ fathoms. The American lobster is not normally found south of Cape Hatteras, but lobsters are frequently taken off Cape Henry, Va. For instance, one 5½-lb. and two 8–10-lb. lobsters were taken by the trawler *Ensign* approximately 45 miles E.N.E. Oregon Inlet, N.C., at 38–45 fathoms, January 21, 1963. In December 1958, an American lobster was caught in a crab pot near Cedar Island, N.C. Mr. Clayton Fulcher, Atlantic, N.C., reported that he tried to get the specimen, but this prize was eaten by the fisherman's family. Hay and Shore (1918) cited one doubtful occurrence of the lobster near Beaufort, N.C.

Munida longipes H. Milne Edwards. South Carolina to Curaçao; 154–338 fathoms (Schmitt, 1935a).

Pagurus cokeri Hay. South of Cape Lookout, N.C., to eastern Gulf of Mexico; approximately 150–200 fathoms.

Catapagurus sharreri Milne Edwards. Between Capes Hatteras and Lookout, N.C., to Barbados; 87–221 fathoms.

Latreillia elegans Roux. Both sides of North Atlantic Ocean, Mediterranean Sea, Natal; 70–200 fathoms (Rathbun, 1937).

Portunus ventralis (Milne Edwards). Georgia or Florida to Brazil; surface and near shore (Rathbun, 1930a).

Portunus sebae (Milne Edwards). Hay and Shore (1918) cited reports of this species in the Carolinas. Gulf of Mexico and Florida Straits to Brazil, Bermuda; surface to 15 fathoms.

Callinectes danae Smith. Status of this species on the southeastern coast of the United States needs clarification for there is no clear distinction there between it and *C. ornatus*. Indian River Inlet, Fla. to Brazil; shallow water to a few fathoms.

Parapinnixa hendersoni Rathbun. This species is questionably recorded from lat. 34°34' N. long. 75°50' W., southeast of Cape Lookout, N.C., 35

TABLE 1.—*Geographic ranges of decapod crustaceans*

[Lower portion of table shows combined totals of species with ranges limited by natural

Families	Number of species	North of Cape Cod to Florida, Gulf of Mexico, West Indies and South America	Cape Cod to east Gulf of Mexico and West Indies	Cape Cod to west Gulf of Mexico and South America	Middle Atlantic States to west Gulf and Caribbean	Middle Atlantic States to South America	Hatteras to east Gulf of Mexico, West Indies, and South America	Hatteras through Gulf of Mexico and West Indies to South America	Hatteras to west Gulf of Mexico
Penaeidae	17				1	3	2	4	2
Pasiphaeidae	1						1		
Palaemonidae	14	1		2		1	1	1	1
Gnathophyllidae	1								
Alpheidae	10	1						5	
Ogyrididae	2				2				
Hippolytidae	8			2	1	1			
Processidae	1								
Pandalidae	1								
Crangonidae	1	1							
Palinuridae	1							1	
Scyllaridae	4							1	
Galatheidae	2								1
Porcellanidae	8			2	1			3	
Callinassidae	3	1							
Paguridae	21	1	1	1		1	5		1
Albuneidae	3								1
Hippidae	2			1					
Raninidae	1								
Dromiidae	3							1	1
Homolidae	1								
Leucosiidae	6				1		1		
Calappidae	9			1	1		1	3	
Portunidae	13	2		3		2		3	
Canceridae	2	2							
Xanthidae	24	3		2	1		3	6	
Goneplacidae	3							1	
Pinnotheridae	10	1	2	3	1				
Palicidae	2							1	1
Grapsidae	6	1		1	1				
Ocypodidae	4	1		3					
Majidae	30		3		1		5	2	
Parthenopidae	6			1		1	2		
Total	220	15	6	22	11	9	21	32	8
		North Cape Cod-South	Cape Cod-South		Middle Atlantic-South		Hatteras-South		
Combined total		15	28		20		61		
Percent total	99.9	6.8	12.7		9.1		27.7		

fathoms (U.S. National Museum). Cuba, Gulf of Mexico; 30-35 fathoms.

Parapinnixa beaufortensis Rathbun. The only specimen of this species known is the holotype from fishing grounds, 20 miles off Beaufort Inlet, N.C. Rathbun (1918b) doubtfully referred this form to the genus *Parapinnixa* and believed that it was a postlarval stage of an unknown species because of small size, relatively large eyes, hairiness of legs and carapace, and thin gripping edges of the fingers suggesting that in another molt or two gaping fingers might emerge. I believe that it may be a young *Palicus*.

Notolopas lamellatus Stimpson. Rathbun (1930a) gave one occurrence of an ovigerous female off Beaufort, N.C. Sonora, Mexico, to Ecuador (Garth, 1958).

A large amount of unidentified material is in existing collections and some of this contains undescribed species. It is expected that the increase in oceanographic research in Southeastern United States will soon add to knowledge of decapod crustaceans in the area.

GLOSSARY

Many of the structures listed alphabetically and defined are shown schematically on figures

occurring in the Carolinas, arranged by family

barriers. Numbers marked with an asterisk duplicate numbers in adjacent columns]

Eastern and western Atlantic	Pacific	Cosmopolitan	Endemic	Disjunct at Florida Peninsula	Lookout to east Gulf of Mexico and West Indies	Lookout to east Gulf of Mexico, West Indies, and South America	Lookout through Gulf of Mexico, West Indies, and South America	Charleston to West Indies, Texas or South America
1+*1	*1	1		*1	1	1	1	
1	*1	2		0				
			1	*4	2	1	1	
	*2			0				
				0	1	1	2	
2				*1				
			1 (restr.)	0			1	1
				0				
	*1			0	1			
				0				
				0	1	2		
				0			1	
	*1			0	1			1
				*2		1	1	
1				*4	2	5	2	2
				*1			1	
				*2				1
				0	1			
1				0		1		
				0				
1				0	3	1		
				0	2			1
				0	1			1
				0				
			1	0	2	1	6	
				0			2	
				*5	1		1	
2	*1	1		*1				
				*2				
1				0	4	6	5	3
				0		2		
10+*1	*7	4	3	*23	23	22	24	10
East and west Atlantic		Cosmopolitan	Endemic		Lookout-South			Charleston-South
10+*1		4	3		69			10
4. 5		1. 8	1. 4	*10. 5	31. 4			4. 5

2, 3, and 4. Other terms not listed are shown on these figures.

Acicle.—Antennal scale which is reduced to a spine.

Afferent channels.—Openings through which water passes to the gills. In brachyuran crabs, usually opening behind the pterygostomian regions and in front of chelipeds except in certain Oxystomata in which they open at anterolateral angles of palate or endostome.

Antennal spine.—Spine on anterior edge of carapace immediately below orbit adjacent to base of antenna (fig. 2).

Anterolateral teeth.—Teeth on anterolateral border of crabs between orbit and lateral spine, exclusive of outer orbital teeth.

Apodeme.—Any cuticular ingrowth of body wall.

Appendix interna.—Small separate branch on medial side of pleopodal endopodite tipped with hooks which interlock with opposite member in swimming.

Appendix masculina.—Accessory male organ located medially on second pair of pleopods between endopodite and appendix interna.

Arthrobranchiae.—Gills attached to articular

membrane between the coxa of an appendage and the body wall.

Basis (basipodite).—Second article (from the body) of a leg or maxilliped. Sixth segment from distal end of the limb.

Basicerite.—Spine on dorsal side of basis of antenna; sometimes more lateral than dorsal.

Branchiocardiac groove.—Groove separating branchial and cardiac regions.

Branchiostegal spine.—Spine on anterior edge of carapace, or near it, immediately below branchiostegal groove (fig. 2).

Branchiostegite.—Part of carapace not coalesced ventrally with the thoracic somites, but overhanging on each side as a covering for chamber in which the gills are concealed.

Buccal cavity.—Cavity on ventral surface of body in which the mouthparts are situated; it is bounded anteriorly by the epistome, laterally by the free edges of the carapace.

Carina.—A keellike ridge or prominence.

Carpus (carpopodite).—Third article from the distal end of a leg.

Cervical groove.—Complex groove or series of grooves running across carapace. It is transverse at the middle, then turns obliquely forward (and outward in brachyurans) to the anterolateral margin.

Chela.—Arrangement of the distal two articles of a crustacean limb by which the terminal element is opposed to the element which precedes it, so that the appendage is adapted for grasping.

In a true chela, the elements are shaped as fingers which close against each other.

In a subchela, the terminal article (dactyl) usually closes against the distal surface of the penultimate article (propodus).

Chelipeds.—Pair or pairs of thoracic legs immediately behind the maxillipeds. They bear chelae, or pincer-claws, and are often stouter, sometimes much stouter, than the succeeding walking legs.

Coxa (coxopodite).—First or proximal article of a leg or maxilliped.

Dactyl (dactylus or dactylopodite).—Terminal or distal article of a leg or maxilliped. The dactyl is the movable finger of a cheliped.

Efferent channels.—Channels through which water passes from the gills. These open at the sides of the endostome, except in the superfamily

Oxystomata in which they open at the middle of the endostome.

Endognath.—Inner or principal branch of a maxilliped.

Endopodite.—Medial ramus of a biramous appendage.

Endostome.—Part of the epistome which forms the palate in brachyurans and is usually separated from the epistome proper by a transverse ridge.

Epibranchial (epibranchial region).—Portion of the porcellanid (crab) carapace which is situated behind the orbit and above the metabranchial region. The region situated between the cervical groove and the *linea anomurica*. There is often a strong spine on the region, referred to as the epibranchial spine.

Epigastric lobes.—Anterior lobes or subregions of the gastric region.

Epimere.—A lateral part of the wall of body somites situated between the tergum and the insertion of appendages.

Epipodite.—Outgrowth of the first seven thoracic coxae.

Epistome.—The antennal sternum is mainly represented by the epistome, a plate of varying shape, lying between the labrum and the bases of the antennae. In Natantia the epistome is comparatively narrow, and on each side is separated from the lateral portions of the carapace by the exhalant branchial channels. In most of the Repantia, the epistome is broad and comes in contact with the carapace on each side; in the Brachyura, it becomes firmly united with the carapace. In this way, there is defined, more or less distinctly, a buccal frame within which lie the mouth parts, and which in most Brachyura is closed by the operculiform third maxillipeds. The sides of this buccal frame are formed by the free anterolateral margins of the carapace.

Exognath.—Outer or secondary branch of a maxilliped.

Exopodite.—Lateral ramus of a biramous appendage.

Fingers (digits).—Narrow scissorlike blades of the claw end of a cheliped, with the movable finger being the dactyl, and the immovable finger the terminal part of the propodus.

Front.—Frontal portion of carapace; that portion of the carapace of a crab which lies between the orbits.

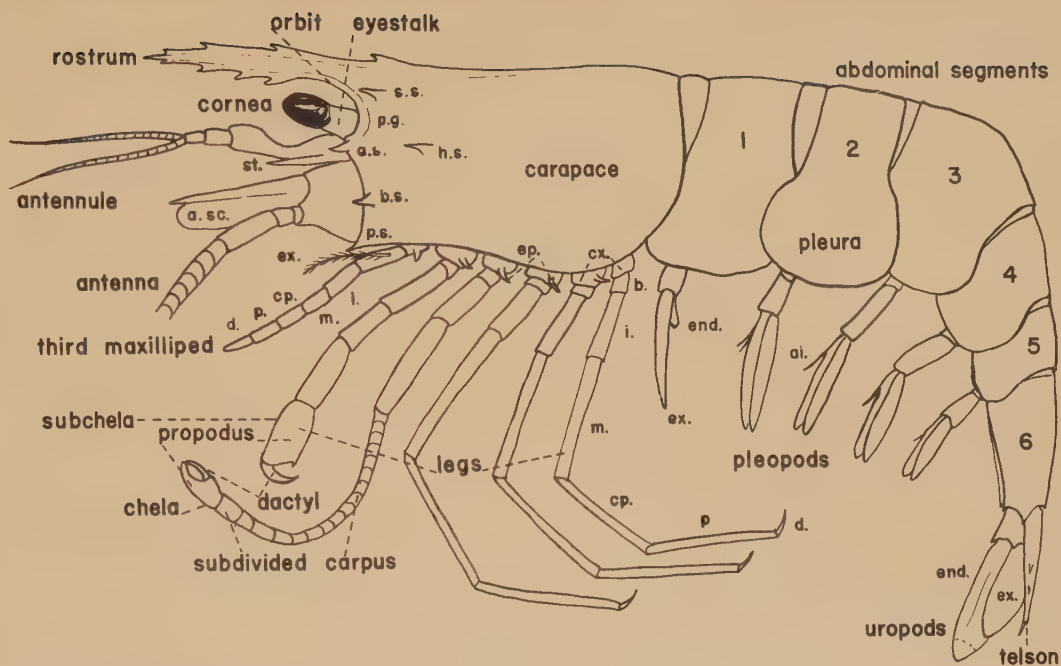


FIGURE 2.—Schematic drawing of shrimp in lateral view; ai., appendix interna; a.s., antennal spine; a. sc., antennal scale; b., basis; b.s., branchiostegal spine; cp., carpus; ex., coxa; d., dactyl; end., endopod; ep., epipod; ex., exopod; h.s., hepatic spine; i., ischium; m., merus; p., propodus; p.g., postorbital groove; p.s., pterygostomial spine; s.s., supraorbital spine; st., stylocerite. (Modified after Holthuis, 1955; Schmitt, 1921.)

Frontal teeth.—True frontal teeth; those teeth originating on the front but exclusive of the inner orbital teeth.

Gastric region.—Large median area, in the crab carapace, bounded behind by the cervical suture, laterally by the hepatic regions, and anteriorly by the frontoorbital regions. It is divisible into the following subregions or lobes: epigastric, proto-gastric, mesogastric, metagastric, and urogastric.

Genital region.—See urogastric lobe.

Hand (chela).—Propodus and dactyl of the cheliped.

Hepatic region.—A small (paired) subtriangular, anterolateral region, wedged between branchial and gastric regions, and either margin of carapace or margin of orbit in Brachyura.

Hepatic spine.—Spine on hepatic region in Natania (fig. 2).

Ischium (ischiopodite).—Fifth article of a leg or maxilliped from the distal end. It is usually the first large article of the maxilliped.

Merus (meropodite).—Fourth article from the distal end of a leg or maxilliped. It is sometimes called the arm of a cheliped.

Mesogastric lobe.—Lobe or subregion which is the median division of the gastric region, pentagonal in form, and with a long, narrow, anterior prolongation.

Metabranhial (metabranhial region).—That region of the porcellanid (crab) carapace which is situated below the *linea anomurica* and, therefore, not completely united with the main portion of the carapace.

Metagastric lobe.—Posterolateral lobe or subregion of the gastric region; often not defined.

Ocellus.—Little eye, distinct from the main organ of vision.

Orbit.—Cavity in the carapace containing the eye.

Orbital region.—Narrow space bordering upper margin of orbit; not always distinguishable.

Palate.—Roof of buccal cavity in crabs.

Palm.—Proximal portion of propodus of chela.

Petasma.—Endopodite of the first pleopods in male Penaeidae. It takes the form of a complicated membranous plate bearing coupling hooks medially which interlock with the member of the

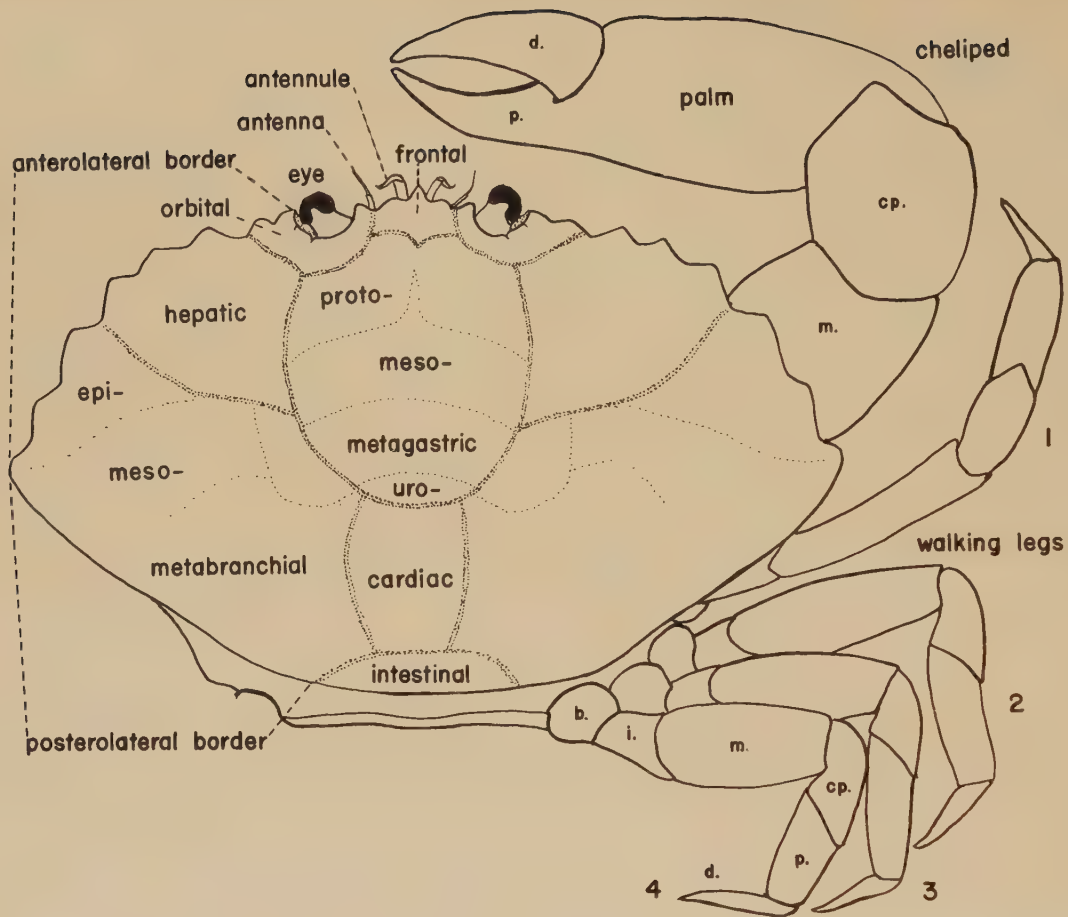


FIGURE 3.—Schematic drawing of brachyuran crab in dorsal view; areas of carapace indicated; legs of right side only shown; b., basis; cp., carpus; d., dactyl; i., ischium; m., merus; p., propodus.

opposite side. The petasma may terminate distally in various combinations of complex-shaped lobes. According to position, these have been termed: distolateral, distoventral, and distomedian. Additional complex processes may also be present.

Pleurobranchia.—Gills attached to lateral wall of body dorsal to the articulation of an appendage.

Podobranchia.—Gills attached to the coxa of an appendage.

Postorbital groove.—Groove on carapace behind orbit and more or less parallel to margin of orbit (fig. 2).

Propodus (protopodite).—Second article from the distal end of a leg or maxilliped. In a cheliped, the propodus consists of a palmar portion and a narrower, immovable finger.

Prosartema (dorsal eye brush).—Long, thin, ciliated lobe arising dorsally from proximomedial border of first antennular segment and extending anteriorly; found in family Penaeidae.

Protogastric lobe.—Lobes or subregions which are the anterolateral lobes of the gastric region.

Protopodite.—Peduncle of an appendage; in unmodified form, it consists of one coxal and one basal article.

Pterygostomian region.—Triangular space on ventral surface of carapace, on either side of buccal cavity in Brachyura. Region at anterolateral corner of carapace in Natantia.

Pterygostomian spine.—Spine at anterolateral (anteroventral) corner or border of carapace (fig. 2).

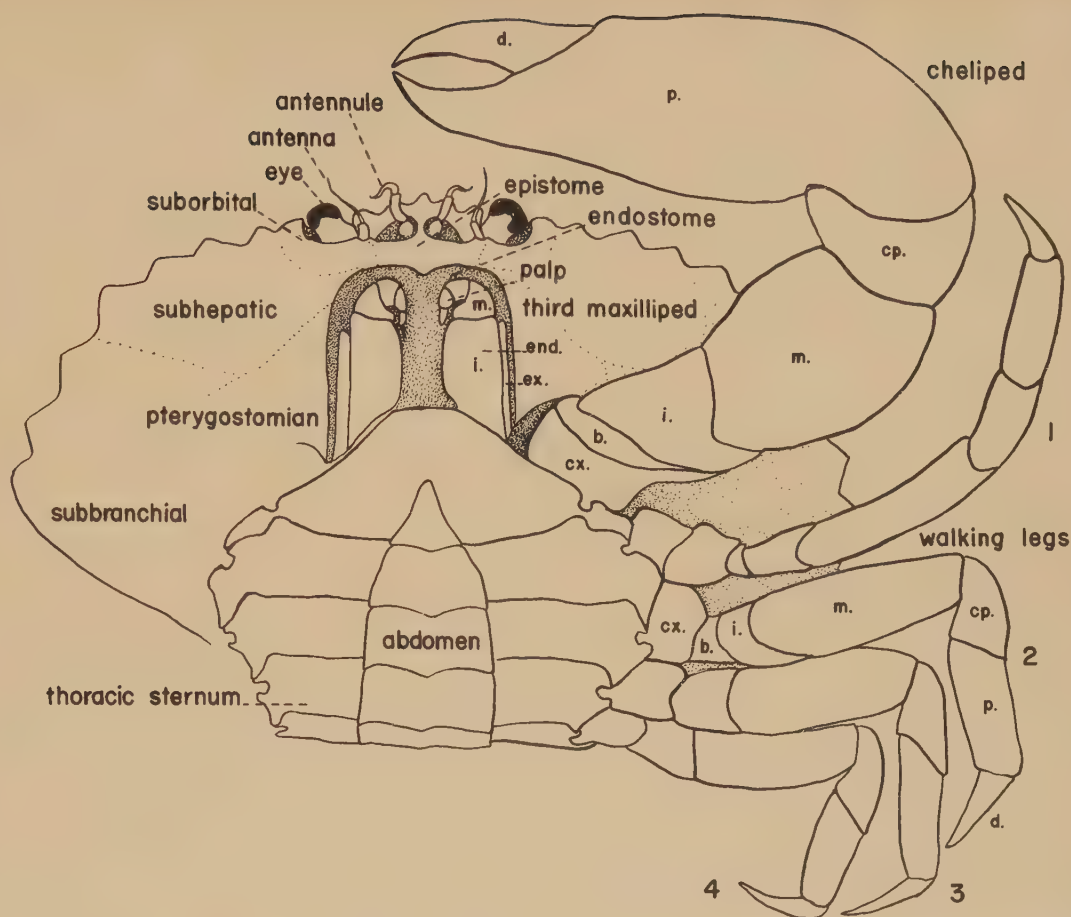


FIGURE 4.—Schematic drawing of brachyuran crab in ventral view; areas of carapace indicated; legs of left side only shown; b., basis; cp., carpus; cx., coxa; d., dactyl; end., endognath; ex., exognath; i., ischium; m., merus; p., propodus.

Scaphocerite.—Antennal scale (fig. 2).

Stylocerite.—Spine or rounded lobe on lateral aspect of basal article of antennules.

Subhepatic region.—Area below the hepatic region and below the anterolateral border of the carapace.

Suborbital spine.—Spine on lower rim of orbit (fig. 2).

Supraorbital spine.—Spine above and behind orbit (fig. 2).

Telson.—Terminal somite of the abdomen except in the Brachyura.

Tergite.—Dorsal plate of a segment.

Thelycum.—External seminal receptacle, variously developed, lying on sternum of the thorax and formed by outgrowths from the last and next

to last thoracic somites.

Urogastric lobe.—Posteromedian lobe or sub-region of the gastric region; sometimes called the genital region.

ORDER DECAPODA

Caridoid facies either retained or greatly modified. Exopodite of maxilla (scaphognathite or bailer) large. First three pairs of thoracic limbs specialized as maxillipeds. Gills typically in several series, attached to coxae of thoracic limbs, to their articular membranes, and to lateral walls of thoracic somites (podo-, arthro-, and pleuro-branchia); rarely absent. Young rarely hatched in nauplius stage (Calman, 1909).

KEY TO SUBORDERS, SECTIONS, SUPERFAMILIES, AND FAMILIES OF DECAPOD CRUSTACEANS FOUND IN THE CAROLINAS

- a. General form shrimplike; abdomen well developed and usually with carapace compressed; pleopods always present in full number and used for swimming..... Suborder Natantia (p. 14).
- b. Pleura of second abdominal segment not overlapping those of first segment..... Section Penaeidea (p. 14).
- c. First three pairs of legs chelate, all five pairs of legs well developed..... Family Penaeidae (p. 14).
- cc. First three pairs of legs chelate, last two pairs of legs small or wanting..... Family Sergestidae (p. 38).
- bb. Pleura of second abdominal segment overlapping those of first segment..... Section Caridea (p. 41).
- c. First pair of legs chelate or simple.
- d. Fingers of chelae on first and second legs slender, cutting edges all pectinate.... Family Pasiphaeidae (p. 41).
- dd. Fingers of chelae on first and second legs variable in thickness; cutting edges of fingers of chelae not all pectinate.
- e. Carpus of second pair of legs entire; first pair of legs always with well-developed chelae.
- f. Third pairs of maxillipeds pediform; body slender in most species..... Family Palaemonidae (p. 42).
- ff. Third pair of maxillipeds broad, leaflike; body short and thick..... Family Gnathophyllidae (p. 61).
- ee. Carpus of second pair of legs usually subdivided into two or more joints; first pair of legs often asymmetrically chelate.
- f. Chelae of first pair of legs distinct, at least on one side.
- g. Each of first legs chelate.
- h. Eyestalks short, usually covered by carapace; first pair of legs stronger than second
Family Alpheidae (p. 62).
- hh. Eyestalks medium length or long, not covered by carapace; first pair of legs not stronger than second pair.
- i. Rostrum small or wanting; eyestalks long, slender; first two pairs of legs subequal
Family Ogyrididae (p. 74).
- ii. Rostrum well developed; eyestalks not abnormally lengthened; second pair of legs usually longer or stronger than first..... Family Hippolytidae (p. 76).
- gg. Only one of first pair of legs chelate, opposite leg ending in a simple clawlike dactyl
Family Processidae (p. 86).
- ff. Chelae of first pair of legs microscopically small or absent..... Family Pandalidae (p. 87).
- cc. First pair of legs subchelate..... Family Crangonidae (p. 88).
- aa. General form lobsterlike or crablike; abdomen either well developed or greatly reduced in size, usually with abdomen and carapace depressed; pleopods reduced or absent, not used for swimming..... Suborder Reptantia (p. 90).
- b. Abdomen extended, symmetrical, with well-developed tail fan..... Section Macrura (p. 90).
- c. Abdomen well armed, pleura well developed; third pair of legs like first..... Superfamily Scyllaridea (p. 90).
- d. Body subcylindrical; antennae with strongly developed flagella..... Family Palinuridae (p. 91).
- dd. Body strongly depressed; antennae short, squamiform..... Family Scyllaridae (p. 94).
- cc. Abdomen more or less membranous; pleura small or wanting; third legs unlike first, never chelate
Superfamily Thalassinidea;
Family Callinassidae (p. 99).
- bb. Abdomen bent upon itself or flexed beneath thorax; pleura usually small or wanting; tail fan variable in development; (third pair of legs unlike first, never chelate).
- c. Uropods usually present, often reduced in size, sometimes united with telson; last thoracic sternite free; carapace not apparently fused with epistome..... Section Anomura (p. 104).
- d. Abdomen well developed.
- e. Abdomen symmetrical, more or less flexed beneath thorax; body depressed; tail fan well developed
Superfamily Galatheaidea (p. 104).
- f. Form somewhat lobsterlike; rostrum well developed..... Family Galatheaidea (p. 104).
- ff. Form crablike (*Euceramus* elongate); rostrum short and broad or wanting.. Family Porcellanidae (p. 106).
- ee. Abdomen asymmetrical; tail fan reduced and adapted for holding body in hollow objects
Superfamily Paguridea; Family Paguridae (p. 114).
- dd. Abdomen much reduced in size and flexed under thorax..... Superfamily Hippidea (p. 136).
- e. First pair of legs subchelate; carapace depressed..... Family Albuneidae (p. 136).
- ee. First pair of legs simple; carapace subcylindrical..... Family Hippidae (p. 139).

KEY TO SUBORDERS, SECTIONS, SUPERFAMILIES, AND FAMILIES OF DECAPOD CRUSTACEANS FOUND
IN THE CAROLINAS—Continued

aa. General form lobsterlike or crablike—Continued

bb. Abdomen bent upon itself or flexed beneath thorax—Continued

cc. Uropods rarely present, never biramous; abdomen small, permanently flexed beneath thorax; carapace fused with epistome; (first pair of legs always chelate or subchelate)----- Section Brachyura (p. 142).

d. Anterior thoracic sterna very broad, posterior thoracic sterna narrow and keellike; posterior thoracic epimera largely exposed by reduction of branchiostegite----- Subsection Gymnopleura; Family Raninidae (p. 142).

dd. Anterior thoracic sterna not usually broad, posterior thoracic sterna not keellike; posterior thoracic epimera covered by branchiostegite.

e. Buccal frame triangular, prolonged forward to form a gutter; openings of oviducts generally sternal; first pleopods lacking in female----- Subsection Oxystomata (p. 146).

f. Afferent branchial openings on either side of endostome----- Family Leucosiidae (p. 147).

ff. Afferent branchial openings in front of bases of chelipeds----- Family Calappidae (p. 152).

ee. Buccal frame roughly quadrate; not prolonged forward.

f. Last pair of legs modified in form and dorsal in position; openings of oviducts coxal; first pleopods present in female----- Subsection Dromiacea (p. 143).

g. Sternum of female with longitudinal grooves; eyes usually completely sheltered by orbits when retracted
Family Dromiidae (p. 143).

gg. Sternum of female without longitudinal grooves; eyes incompletely or not at all sheltered by orbits when retracted----- Family Homolidae (p. 146).

ff. Last pair of legs normal in position (rarely reduced or dorsal, Palicidae); openings of oviducts on sternum; first pleopods lacking in female----- Subsection Brachygnatha (p. 160).

g. Body of medium width or broad in front; rostrum reduced or wanting.

Superfamily Brachyrhyncha (p. 160).

h. Carpus of third maxillipeds articulating at or near anterointernal angle of merus; body usually round or transversely oval; openings of vasa deferentia nearly always coxal.

i. Distal articles of last pair of legs broad, thin and paddlelike----- Family Portunidae (p. 160).

ii. Distal articles of last pair of legs not paddlelike.

j. Antennules folding longitudinally; outer maxillipeds long, overlapping epistome

Family Cancridae (p. 174).

jj. Antennules folding transversely or obliquely; outer maxillipeds usually not overlapping epistome.

k. Body usually transversely oval; openings of vasa deferentia rarely sternal

Family Xanthidae (p. 176).

kk. Body usually quadrate; openings of vasa deferentia sternal or, if coxal, passing along groove in sternum----- Family Goneplacidae (p. 201).

hh. Carpus of third maxillipeds not articulating at or near inner angle of merus; body usually quadrate (except Pinnotheridae); openings of vasa deferentia nearly always sternal; right chela not always larger than left (except Palicidae).

i. Small, usually commensal crabs with small eyes and orbits; body usually somewhat rounded, adult females often with carapace somewhat membranous----- Family Pinnotheridae (p. 203).

ii. Free living crabs with eyes not strikingly reduced; body usually quadrate, adult females with carapace normal.

j. Last pair of legs dorsally placed and weaker than others; interantennular septum very thin
Family Palicidae (p. 215).

jj. Last pair of legs not dorsally placed; not markedly weaker than others; interantennular septum not very thin.

k. Front broad; eyestalks of moderate length or short; a gap of varying size between outer maxillipeds----- Family Grapsidae (p. 217).

kk. Front with moderate width; eyestalks long; outer maxillipeds nearly, or quite, closing buccal area----- Family Ocypodidae (p. 225).

gg. Body narrowed in front; rostrum usually distinct; orbits often incomplete

Superfamily Oxyrhyncha (p. 235).

h. Chelipeds not much larger than other legs----- Family Majidae (p. 236).

hh. Chelipeds much larger than other legs----- Family Parthenopidae (p. 266).

Systematic and Ecological Discussion

Suborder Natantia

Body almost always laterally compressed. Rostrum usually compressed and serrated. First abdominal segment not much smaller than rest. Antennules generally with stylocerite; antennal scale generally large and lamellar. Legs usually slender, except sometimes a stout chelate limb or pair, which may be any one of first three pairs; with basipodite and ischiopodite very rarely coalesced and with only one fixed point in carpopodal articulation (with some doubtful exceptions); sometimes with exopodites; podobranchiae hardly ever present on first three and never on last two pairs; male genital apertures in articular membrane. Pleopods always present in full number, well developed, used for swimming (Calman, 1909).

Section Penaeidea

Pleura of second abdominal segment not overlapping those of first segment. Antennules generally with stylocerite. Mandibular palps straight. First maxillipeds without expansion at base of exopodite, endopodite long; second maxillipeds with terminal articles normal; third maxillipeds with seven articles. Third legs chelate (except when much reduced), not stouter than first pair. First pleopods of male bearing sexual apparatus (Calman, 1909).

Family Penaeidae

Body somewhat or considerably compressed. Rostrum usually well developed, laterally compressed, often with teeth. Eyes moderate or greatly elongate. Antennules with two flagella; basal article of peduncle hollowed out dorsally for eye, with stylocerite on basal outer margin. Mandible with incisor process and palp of one or two articles. First three pairs of legs similar, chelate, slender, increasing in length posteriorly; fourth and fifth legs well developed, simple (Schmitt, 1921).

Remarks.—For most species treated in this handbook information on natural history is included in the separate species accounts. In the

case of parasites found in certain penaeids, such citation has proved too cumbersome. Parasites in this group have been studied only recently. Host specificity and life cycles of the parasites are imperfectly known and identification of some forms is uncertain. The interested student is referred to a review of most of the known parasites given by Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn (1959), and Iversen and Manning (1959).

Spelling of the name *Penaeus* and related generic names has unfortunately not been uniform. Gunter (1957) reviewed these circumstances and re-emphasized that under the International Code, original spelling must be observed. He included a list of the genera of Penaeidae.

KEY TO SUBFAMILIES IN THE CAROLINAS

- a. Postorbital spine present-----Solenocerinae (p. 14).
- aa. Postorbital spine absent.
 - b. Carapace without a median dentate crest, except occasionally over eyes-----Penaeinae (p. 17).
 - bb. Carapace with a median dentate crest extending nearly or entirely to posterior margin
Sicyoninae (p. 32).

Subfamily Solenocerinae

Carapace with postorbital spine, cervical groove extending nearly or quite to dorsum. Ocular peduncle with a distinct tubercle, a scale at external angle of ocular somite. Antennular peduncle with an enlarged ciliated protuberance on inner proximal margin of basal article. First chelipeds with tuft of setae on propodus in both sexes. Coxae from second maxillipeds to fifth legs with weakly forked epipodites. A functional filamentose anterior arthrobranch on 13th somite (4th leg); pleurobranches behind 9th somite (3d maxilliped). Exopodites on maxillipeds and legs. Pleopods, except first pair, biramous. Telson with well-developed terminal point and a pair of subterminal fixed spines (Burkenroad, 1934b).

KEY TO GENERA AND SPECIES IN THE CAROLINAS

- a. Antennular flagella hollowed out medially, channellike in structure-----*Solenocera atlantidis* (p. 15).
- aa. Antennular flagella not hollowed out medially nor channellike in structure
Hymenopenaeus tropicalis (p. 15).

Genus *Solenocera* Lucas, 1849

Burkenroad, 1934b, p. 64.—1936, p. 120.—1939, p. 6.

Solenocera atlantidis Burkenroad

Figure 5

Solenocera atlantidis Burkenroad, 1939, p. 10.

Recognition characters.—Body compressed, carapace deeper than broad; integument thin, smooth; sides of rostrum and area near base of rostrum covered with short hairs; carapace with small pterygostomian spine meeting frontal margin at right angle, spine sometimes doubled; postorbital and hepatic spines well developed; antennal angle acute, more or less toothlike, often not greatly produced; orbital angle with a distinct spine on margin; cervical groove reaching mid-dorsal line; branchiocardiac groove prominent. Rostrum not reaching distal edge of eye; lower margin unarmed, convex; with five to seven, usually six, dorsal teeth not counting dagger-shaped tip, two behind, one above orbital margin, posterior tooth slightly remote from others. Post-rostral carina not continued beyond crossing of cervical groove. Antennular flagella slender, about half as long as body; lower flagellum broader than upper at hollowed basal portion. Antennal scale extending no more than one-tenth its length beyond antennular peduncle.

Coxa of fifth legs with strong tooth on antero-medial margin in both sexes.

Abdomen with last three segments carinate; third to fifth segments cleft posterodorsally at midline; sixth segment with a spine at middorsal posterior and posterolateral corners and a tooth-like projection at middle of distolateral edge. Telson short, broad, lateral spines large. Exopods of uropods with no spine at distolateral corner.

Measurements.—Length of body: large male, 87 mm.; large female, 56 mm.

Variations.—The epipodites are usually mitten-shaped, but sometimes more distinctly forked, the thumb or inferior branch never exceeding the proximal or palmar portion of the blade, exclusive of the peduncle.

Color.—Orange red, color most concentrated as bands across posterior parts of abdominal tergites (Burkenroad, 1939).

Habitat.—Mud, shell, and coral bottoms; 10 to 80 fathoms.

Type locality.—Gulf of Mexico off Alabama (*Atlantis* station 2813, roughly lat. 30° N. long. 88° W.), 19 fathoms.

Known range.—Cape Hatteras, N.C., to near Campeche, Mexico; Surinam (Hildebrand, 1955; Holthuis, 1959).

Remarks.—Females with well-ripened ovaries have been taken in March off Alabama (Burkenroad, 1939).

Genus *Hymenopenaeus* Smith, 1882

Burkenroad, 1936, p. 102.

Hymenopenaeus tropicalis (Bouvier)

Figures 6–7

Parartemesia tropicalis Bouvier, 1905, p. 749.

Haliporus tropicalis: Bouvier, 1906, p. 4.—Milne Edwards and Bouvier, 1909, p. 247, pl. 3, figs. 1–9, text-figs. 45–54.

Hymenopenaeus tropicalis: Burkenroad, 1936, p. 102.

Solenocera weymouthi Lindner and Anderson, 1941, p. 181, fig. 1.

Recognition characters.—Body robust, laterally compressed; integument thin, polished, except finely setose at sides of rostrum and area near base of rostrum; carapace deeper than broad with antennal, hepatic, and postorbital spines well developed, a small stout spine on orbital margin; cervical groove extending nearly to middorsal line; branchiocardiac groove extending from near anterolateral corner to level of base of first legs. Rostral crest not extending beyond level of cervical groove, armed above with 7 to 10 teeth excluding rostral tip, posterior tooth slightly remote from others; rostrum reaching about to distal edge of eye, straight or slightly upturned at tip, lower edge convex, unarmed, ciliated. Prosartema prominent, hairy, extending to or beyond middle of second segment of antennular peduncle. Antennular flagella somewhat flattened, upper ramus about one-third diameter of lower at base. Antennular flagella about three times body length.

Female with projections on coxae of last three pairs of legs, first pair posteromedial and blunt pointed; second pair medial, bladelike, with thin, styliform posterior projection; third pair medial, broad, bladelike, partially covering thelycum. Thelycum setose, posterior lateral lobes united; middle lobes rounded, discrete; anterior lobes closely approximated at midline, partially covered by coxal projections of fourth legs.

Abdomen with middorsal carina low and faint on third segment, progressively more prominent

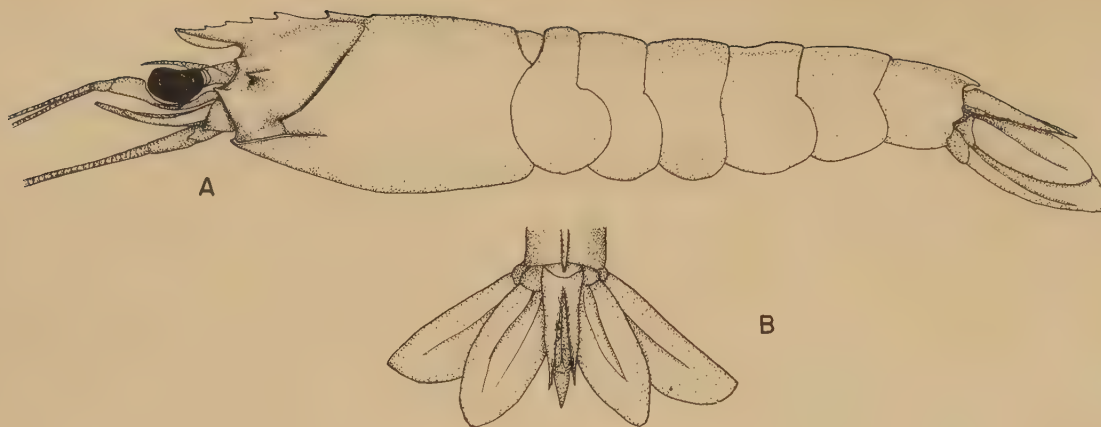


FIGURE 5.—*Solenocera atlantidis* Burkenroad. A, animal in lateral view; B, uropods and telson in dorsal view; A-B $\times 2.5$.

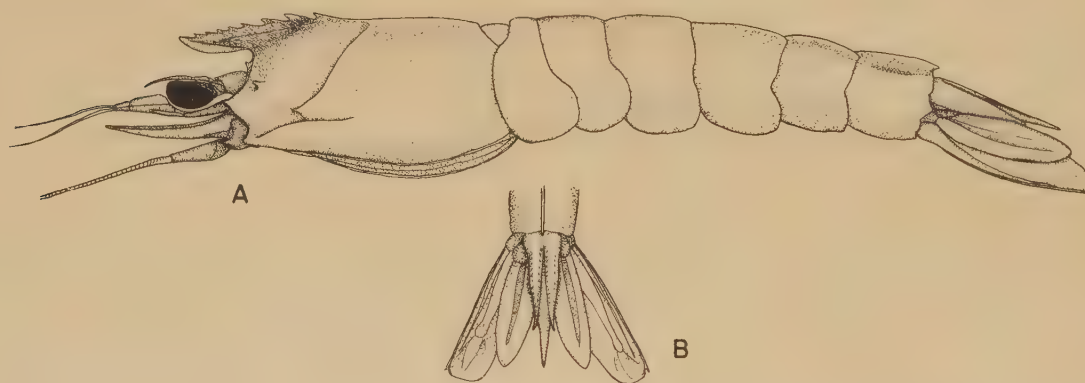


FIGURE 6.—*Hymenopenaeus tropicalis* (Bouvier). A, animal in lateral view; B, uropods and telson in dorsal view; A-B $\times 1.25$.

posteriorly; segments three to five variably cleft posterodorsally; sixth segment with a small mid-dorsal posterior spine, a spine at posterolateral corners, and a toothlike projection at middle of distolateral edge. Telson tapering to a strong point flanked on each side by a strong, fixed, sub-terminal spine; middorsal groove bifurcated at midlength, forks ending medial to base of fixed spines. Exopods of uropods with small spine at distolateral corner. Male with large, membranous, complexly folded petasma; tips of petasma reaching base of second legs.

Measurements.—Length of body: large male, 56 mm.; large female, 92 mm.

Color.—Red.

Habitat.—Seventeen to 200 fathoms, rarely deeper; usually inside 100-fathom curve.

Type locality.—Florida Bank (Gulf of Mexico), lat. $26^{\circ}31' N$. long. $85^{\circ}03' W$.

Known range.—Cape Hatteras, N.C., to Gulf of Mexico, off Alabama.

Remarks.—Burkenroad considered it likely (in Anderson and Lindner, 1945) that *Solenocera*



FIGURE 7.—*Hymenopenaeus tropicalis* (Bouvier). Petasma of male in ventral view, 1 mm. indicated.

weymouthi Linder and Anderson was identical with *Hymenopenaeus tropicalis* (Bouvier). Comparison of a number of specimens of both forms leads me to regard them as identical. Prominence of the coxal projections on the last three pairs of legs in females varies with age. Those illustrated by Lindner and Anderson appear not so well developed as in fully matured *H. tropicalis* females.

Subfamily Penaeinae

Carapace without postorbital spine; cervical groove not extending to dorsum. Ocular somite without a greatly produced pair of median pro-

jections, but with a more or less conspicuous pair of projections from lateral portions; ocular peduncles with some inconspicuous vestiges of a median tubercle. Proximomedian margin of antennular peduncle produced as an elongate scale. First chelipeds with tuft of setae on propodus in both sexes. No podobranchs behind eighth somite (second maxillipeds). No epipodites behind 12th somite (3d legs); epipodites usually forked. No filamentous anterior arthrobranch on 13th somite (4th leg). Pleopods, except first pair, biramous. Telson with well-developed terminal spine (Burkenroad, 1934b).

KEY TO GENERA AND SPECIES (PARTIAL) IN THE CAROLINAS

- a. Rostrum with ventral teeth-----*Penaeus* (p. 17).
- aa. Rostrum without ventral teeth.
 - b. Telson with subterminal pair of fixed spines.
 - c. Carapace with longitudinal and transverse sutures present; body nearly smooth
Parapenaeus longirostris (p. 27).
 - cc. Carapace without longitudinal and transverse sutures; body pubescent-----*Penaeopsis goodei* (p. 29).
 - bb. Telson with no subterminal pair of fixed spines.
 - c. Rostrum slender, sinuous, as long as or longer than carapace, with basal thin, high crest armed with five teeth plus an isolated epigastric tooth-----*Xiphopenaeus kroyeri* (p. 30).
 - cc. Rostrum not slender and sinuous, about half length of carapace, dorsal teeth evenly spaced
Trachypenaeus constrictus (p. 31).

KEYS TO SPECIES IN THE CAROLINAS

Genus *Penaeus* Fabricius, 1798

Burkenroad, 1934b.—Hemming, 1958b.

Adults

(Based on keys by Anderson and Lindner, 1945, and Voss, 1955)

- a. Lateral rostral grooves not extending beyond base of rostrum-----*setiferus* (p. 18).
- aa. Lateral rostral grooves reaching almost to posterior margin of carapace.
 - b. Petasma of male with external edge of distoventral lobe armed with 2 to 12, usually 4 to 7, spinules; teeth of internal edge of lobe long and sharp in close-set group of 6 to 16. Thelycum of female with anteromedian corners of lateral plates moderately gaping, not covering carina of posteromedian part of median plate on 13th body somite (4th legs)-----*duorarum* (p. 21).
 - bb. Petasma of male with external edge of distoventral lobe smooth, incurved, teeth of internal edge of lobe small, in close-set group. Thelycum of female with anteromedian corners of lateral plates widely gaping, exposing forked carina of posteromedian plate on 13th body somite (4th legs)-----*aztecus* (p. 24).

JUVENILES BETWEEN 17 AND 47 MM. TOTAL LENGTH, LIVE OR FRESHLY PRESERVED

(Williams, 1953)

- a. Lateral rostral grooves not reaching almost to posterior margin of carapace; rostrum prominent and slightly upturned at tip in individuals above 22 mm. total length. Ground color light gray, sometimes with greenish cast in shrimp taken from beds of vegetation; chromatophores (widely spaced except on spines, ridges, and uropods) colored slate-blue and brown; uropods with reddish-brown to brown areas distally-----*setiferus* (p. 18).
- aa. Lateral rostral grooves reaching almost to posterior margin of carapace (shallow in 17 mm. individuals). Color gray to light brown, sometimes with greenish cast in shrimp taken from beds of vegetation; chromatophores numerous and closely spaced, often in bands or patches.
 - b. Rostrum usually not upturned at tip. Chromatophores slate-blue and brown; usually with conspicuously pigmented lateral spot at juncture of third and fourth abdominal segments; uropods with uniform sprinkling of chromatophores, degree of transparency uniform throughout (color more dense in older individuals)
duorarum (p. 21).
 - bb. Rostrum usually slightly upturned and attenuate at tip. Chromatophores brown and olive-green; uropods with reddish-brown to brown areas distally-----*aztecus* (p. 24).

Penaeus setiferus (Linn.). White shrimp

Figures 8-9

? *Cancer setiferus* Linnaeus [in part]. 1767, p. 1054.

Penaeus setiferus: Hay and Shore, 1918, p. 378, pl. 25, fig. 5.—Burkenroad, 1939, p. 17 (rev.).—Holthuis, 1962, pp. 115-118.

Penaeus fluviatilis: Gunter, 1962a, b, pp. 107-114; 118-121.

Recognition characters.—Integument thin, polished, translucent. Carapace with a high median carina continuous anteriorly with rostrum and extending back about two-thirds length of carapace; not grooved posteriorly, with lateral grooves terminating near posterior tooth in rostral series; armed with 9 or 10 sharp teeth dorsally, anterior 6 teeth on rostrum proper; postocular crest absent. Rostrum with tip long, slender, unarmed, up-curved distally, apex sometimes depressed, first dorsal tooth near distal edge of eye, ventral edge armed with two teeth. Antennal spine surmounting lateral carina extending upward short distance from hepatic spine. Medial antennular flagellum of adult male dorsoventrally flattened and armed dorsally with two sizes of teeth.

Anterolateral marginal ridges of last thoracic sternite of female extending conspicuously mediad near middle of segment making an interrupted crescentic transverse ridge with concavity directed forward; posterior portion of sternite with conspicuous pair of fleshy protuberances. Posterior

margin of 12th sternite with pair of posteromedial convexities extending almost level with median portion of margin.

Abdomen with fourth to sixth segments carinate; carina of sixth segment with a groove on each side. Telson with deep median groove and an acuminate tip. Ventral margin of pleura of first abdominal segment almost straight. Petasma of male with diagonal ridge across face of distolateral lobe.

Measurements.—Length of body: large male, 182 mm.; large female, 197 mm.

Color.—Body translucent, bluish white with dusky bands and patches composed of scattered black specks; rostrum and sides tinged with pink; blades of pleopods marked with dark red; antennae dark brown; uropods with tips of blades dark brownish purple with narrow stripe of yellowish green along margin.

Habitat.—Estuaries and inner oceanic littoral, predominantly on mud bottom from water's edge to 17 fathoms off Atlantic coast; rarely to 43 fathoms in Gulf of Mexico (Springer and Bullis, 1952).

Type locality.—Off Matanzas Inlet, Fla.

Known range.—Fire Island, N.Y., to Cape Canaveral, Fla.; Gulf of Mexico from Pensacola, Fla., to Campeche, Mexico; Cuba; Jamaica.



FIGURE 8.—*Penaeus setiferus* (Linnaeus). Animal in lateral view; approximately 25 mm. indicated (after Rathbun, 1884).

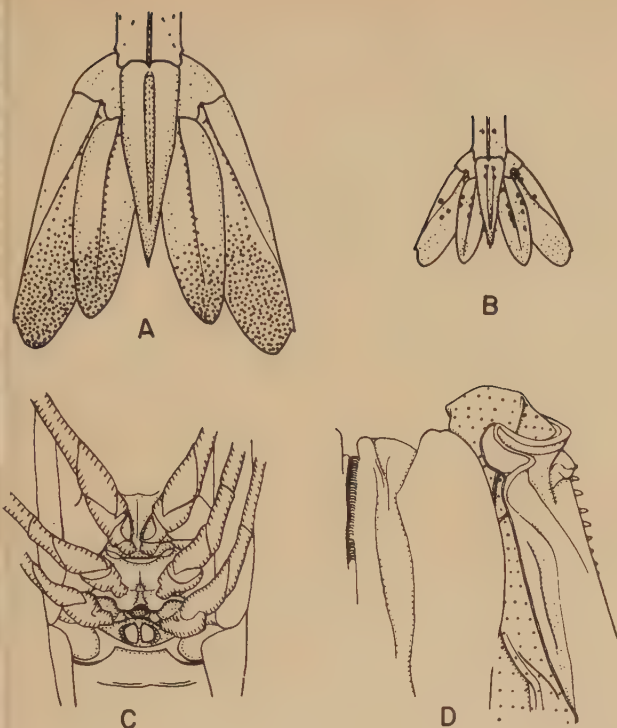


FIGURE 9.—*Penaeus setiferus* (Linnaeus). Chromatophore distribution in tail fan (semidiagrammatic) of A, 17 mm. juvenile, B, 32 mm. juvenile; A-B approximately $\times 5$ (after Williams, 1953). C, thelycum of adult female; D, petasma of adult male, ventral view, distal portion of left half (after Burkenroad, 1934b).

Remarks.—Of the shrimps occurring in the Carolinas, *P. setiferus* has been studied most extensively. This has resulted from the fact that the species has great commercial value, and was the first of the American penaeids to be extensively marketed for food. In the early 1930's, when popular demand caused fishing effort to expand greatly, concern over the possibility of depleting the resource led the U.S. Fish and Wildlife Service to initiate a research program on various aspects of the biology of this species. At that time, *P. setiferus* composed over 95 percent of the commercial catch (Lindner and Anderson, 1956). A voluminous literature, scholarly and popular, has accumulated in the ensuing 30 years, and though it would be presumptuous to attempt a complete review of this work here, the chief results of studies can be outlined. (An exhaustive bibliography has been compiled by Chin and Allen, 1959).

Recently (see synonymy) usage of the name *setiferus* for the white shrimp in North America has been questioned. The well-established name *setiferus* would seem best retained here.

The species is caught commercially throughout most of its geographic range (from North Carolina to Mexico); however, by far the greatest concentration occurs in Louisiana, in and near the Mississippi River Delta, and it was here that Viosca (1920) first worked on some aspects of the species' natural history anticipating in many respects later more detailed studies.

One of the latest studies to be published should be cited at the outset. Young (1959) in his exhaustive morphological study of *P. setiferus* reiterated the generalized structure of the Penaeidae. This work is profusely illustrated and the text illuminates details which have often been obscurely presented in older works. Complexes such as the branchial apparatus and associated structures are clearly delineated, as are the skeletal, muscular, nervous, circulatory, and respiratory systems in general. The genital armature, of great taxonomic value, is treated briefly, and here the student must look to the works of Burkenroad (1934b, 1939) for details.

In 1956, Lindner and Anderson summarized work of the U.S. Bureau of Fisheries and the Fish and Wildlife Service in the 1930's and 1940's that had been presented in a series of shorter articles. Reference to this paper will lead the reader to earlier detailed studies.

Spawning of the white shrimp in the Carolinas probably begins in May and extends into September (Lindner and Anderson, 1956; Williams, 1955a); farther south in the Gulf of Mexico the season probably extends from March to September or October. Gunter (1950) suggested two periods of spawning (spring and fall) for Texas waters, but in the Carolinas there is probably only one.

Maturation of gonads has been studied in detail (King, 1948) in both males and females. In females, the stages of maturity can be judged macroscopically by color of the ovary. The earliest or undeveloped stage may last for an indeterminate period of time (Lindner and Anderson, 1956); the developing stage is judged to last a month or less. The succeeding yellow stage persists for 1 to 2 months, and the ripe, olive-drab colored ovaries become spent in less than a month.

Spent ovaries were found to revert to the yellow stage in a period of a few days and then to develop toward a ripened stage again in 2 or 3 months. A large female is estimated to produce a half million to a million eggs at a single spawning (Anderson, King, and Lindner, 1949).

It was thought that studies of the ovary would lead not only to discovery of spawning grounds but also to knowledge of how many times a female shrimp might spawn, and to the approximate age and length of life of the shrimp. Such hopes were incompletely realized. The likelihood of multiple spawning and absence of permanent scars or walled-off areas in the ovary precluded aging by this method. It is possible, but not proved, that a shrimp can spawn more than once in a season. Occurrence of ripe females suggests that spawning in Louisiana takes place offshore in depths greater than 4.5 fathoms, probably between 5 and 17 fathoms. Heegaard (1953) reported occurrence of spawning 6 or more miles from shore in from 10- to 15-fathom water in Texas. The exact location of spawning grounds off the Carolinas remains unknown.

Developmental stages of the white shrimp were elaborated in detail by Pearson (1939), based on plankton tows off the Mississippi River Delta and the coasts of South Carolina, Georgia, and Florida, and on rearing experiments with material taken from plankton catches at St. Augustine Inlet, Fla. (The eggs of penaeids are not carried on the pleopods of the females as in other decapods, but are broadcast.) In this study, few eggs were found, but this circumstance was attributed to the fact that the eggs are demersal, hence, hard to capture, and perhaps deposited chiefly beyond the area sampled. Of the material available for rearing, 5 of 15 eggs hatched within 24 hours after capture. Developmental stages prior to hatching were described, and, following hatching, five naupliar, three protozoal, two mysis, and a series of postlarval stages were described. Pearson thought it likely that though the larvae are more or less at the mercy of currents in the environment, they still are capable of considerable independent movement. From the spawning place at sea, a great number of the larvae move inshore and enter estuaries at about the second postlarval stage (7 mm. total length), and it is at this stage that they abandon planktonic

for a benthonic existence. The length of larval existence from time of hatching to entrance into estuaries was judged to be about 2 or 3 weeks.

Heegaard (1953), studying wild populations of larval white shrimp, and Johnson and Fielding (1956), studying populations reared in captivity, gave somewhat different interpretations of this portion of development. Heegaard suggested that the number of molts in certain portions of the larval history may vary individually; Johnson and Fielding, while agreeing with Pearson's descriptions of stages, gave evidence for shorter time of development from hatching to first post-larva (about 2 weeks). They also gave evidence for very rapid growth of the young, 2.1 mm. and 1.7 mm. per day in different experiments under conditions of full feed. The same authors secured good growth in both high and medium salinities.

Bearden (1961) demonstrated that postlarval *P. setiferus* enter South Carolina sounds from June through September, a period similar to the supposed recruitment period in North Carolina (Williams, 1959).

Once in estuaries on so-called "nursery grounds" the young grow rapidly. Williams (1955a) estimated an average increase in length of 36 mm. per month (1.2 mm. per day), and other estimates of similar nature have been made (Gunter, 1956; Loesch, 1957). The young, which in the early part of their benthonic existence tend to seek the fresher, shallower portions of estuaries, move gradually into deeper, saltier water as they grow, and with approaching maturity they return to sea. Hoese (1960) suggested that migration to estuarine nursery grounds may not be essential to development in this species, but Gunter (1961) gave much evidence to the contrary. Most of the individuals that grow to maturity appear to live a year or a little longer. Some exceptional individuals in the deeper portion of the range may live to be about 2 years old. Mature females attain a larger size than mature males. Lindner and Anderson (1956) estimated that mature *P. setiferus* grow at a rate of about 20 mm. per month during the period March to October.

In addition to annual cyclic movements of larvae into estuaries, and subsequent movement of subadults back to sea, tagging experiments have indicated that *P. setiferus* may make coastwise migrations of considerable length. In their ana-

lysis of these experiments, Lindner and Anderson (1956) showed that in fall and winter, shrimp tend to move south along the Atlantic coast; in late winter and early spring, there is a return movement; and during late spring and summer, position of the population is relatively static. Large individuals are prone to move longer distances than small shrimp. The longest recorded southward movement was by a shrimp tagged at Beaufort, N.C., in October, and recovered 95 days later off Florida, 360 miles from the point of release. The greatest counter movement was from Cape Canaveral, Fla., in January, to South Carolina 168 days later, a distance of 260 miles.

Distribution of *P. setiferus* is not uniform, and this may be conditioned by a number of factors. These are usually thought to be salinity, temperature, and substrate. The young may utilize waters of somewhat lower salinity than the young of related penaeids (Burkenroad, 1934b; Williams, 1955a). Hildebrand and Gunter (1953) and Gunter and Hildebrand (1954) demonstrated a strong positive correlation between the white shrimp catch for a given year and total rainfall for that year and the 2 preceding years in Texas, high rainfall being followed by good catches. In colder portions of the year no young are found in inside waters, at least in the Carolinas (Williams, 1955a). *Penaeus setiferus* is usually found on a muddy substrate on trawling and nursery grounds (Springer and Bullis, 1954; Hildebrand, 1954, 1955), and in experimental tanks it has been shown to choose muddy substrates in preference to sandy or rocky bottoms even though it burrows

to a lesser extent than its near relatives (Williams, 1958).

In recent years the subadult populations of white and other penaeid shrimp in estuaries have been exploited for fish bait. Studies of such fisheries have given more detail on migrations and density of population (Loesch, 1957) and on individual length-weight relationships (Chin, 1960).

Penaeus duorarum Burkenroad. Pink, spotted, brown spotted, or grooved shrimp

Figures 10-11

Penaeus brasiliensis: Hay and Shore [in part], 1918, p. 377, pl. 25, fig. 6.

Penaeus duorarum Burkenroad, 1939, p. 31, figs. 18, 19, 23, 25-27 (rev.).

Recognition characters.—Integument thin, polished, translucent. Carapace with a median carina continuous anteriorly with rostrum and extending nearly to posterior border of carapace, flanked on each side by a broad, rounded groove; posterior half of carina with a median longitudinal groove; anterior half arcuate, highest above orbit and with 9 or 10 sharp teeth; posterior tooth remote from others, anterior 6 or 7 on rostrum proper. Lower margin of rostrum with two to three teeth (occasionally one); tip slender, horizontal or directed slightly downward, unarmed. Anterior margin of carapace with strong antennal spine on carina extending backward nearly to well-developed hepatic spine. Cervical groove extending halfway from hepatic spine to dorsal carina. A subhorizontal suture below hepatic spine, and a groove extending from near hepatic spine to near base of ocular peduncle. An orbital ridge behind eye.



FIGURE 10.—*Penaeus duorarum* Burkenroad. Animal in lateral view with part of appendages removed, "Form A" from North Carolina; natural size.

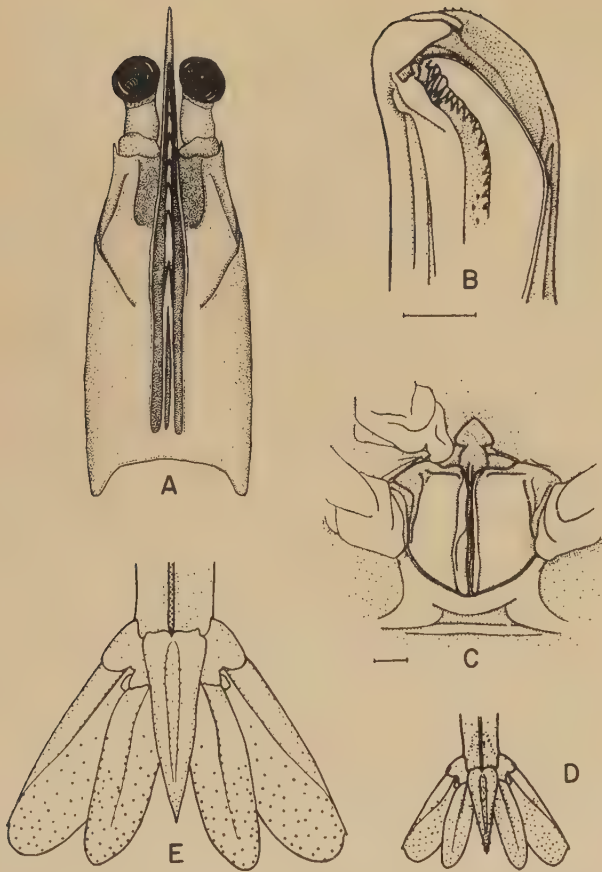


FIGURE 11.—*Penaeus duorarum* Burkenroad. A, carapace and eyes of animal in dorsal view, "Form A" from North Carolina, natural size; B, petasma of adult male, distal portion, view from right side; C, thelycum of adult female; B-C, 1 mm. indicated (after Burkenroad, 1939). Chromatophore distribution in tail fan (semi-diagrammatic) of D, 17 mm. juvenile, E, 32 mm. juvenile; D-E, approximately $\times 5$ (after Williams, 1953).

Female with thelycum composed of two broad lateral plates, and a median plate. Posteromedian part of median plate of adult with a well-developed, short, longitudinal carina extending anteriorly toward roughly semicircular, concave anterior portion. Lateral plates produced medially to meet in midline, except variably divergent at anteromedian corners, thus exposing carina of median plate.

Abdomen with segments four to six carinate, carina of sixth ending posteriorly in a spine and flanked on each side by a narrow groove. Telson with deep median groove and an acuminate tip.

Petasma of male with distal ends of distoventral lobes curved medially, not projecting free of distolateral lobes; external edge of distoventral lobes with a series of 2 to 12, usually 4 to 7, small spinules; median or attached edge of distoventral lobes with a compact group of 6 to 16 large, long, sharp, curved spines; fold of distolateral lobe rather small and armed inconspicuously if at all.

Measurements.—Length of body: large male, 167 mm.; large female, 210 mm.

Variations.—Burkenroad (1939) divided the species into two "Forms," "A" and "B."

In "Form A" the dorsolateral grooves of the sixth abdominal segment usually are almost or entirely closed, though they may be open to a width of one-third the distance from their dorsal lip to the midline.

In "Form B" the dorsolateral grooves of the sixth abdominal segment are broadly open, their width being from one-half to more than equal the distance from their dorsal lip to the midline.

The rostrum is relatively shorter and deeper in old individuals than in young ones. It extends to the end of the basal antennular article in average-sized adults. The rostrum in *P. duorarum* is less sinuous and slender than in *P. aztecus*.

Color.—Juveniles and young adults from estuaries or oceanic water near shore are usually gray, reddish brown or bluish gray of various shades, with a more or less distinct spot of darker color at the pleural juncture of the third and fourth abdominal segments. In juveniles or young adults, this spot and other bandings may be gray, blue gray, blue, or purplish. The tail fan is nearly transparent and edged with blue. In older individuals, especially from deeper oceanic water, the colors tend to be red, pinkish, blue gray or nearly white. The abdominal spots are usually red (Broad, 1950) or lacking entirely. Detailed coloration of the young has been given by Williams (1953).

Habitat.—Estuaries and inner oceanic littoral, predominantly on sand, shell-sand or coral-mud bottom from water's edge to 28 fathoms; rarely 40 to 200 fathoms (U.S. Fish and Wildlife Service, 1960).

Type locality.—Off Alabama (*Atlantis* station 2813, roughly lat. 30° N. long. 88° W.), 19 fathoms.

Known range.—Chesapeake Bay through Gulf of Mexico and West Indies to Brazil; Bermuda; West Africa, from Mauritania to Angola.

"Form A," Chesapeake Bay to Campeche, Mexico; Bermuda. "Form B," Cuba through West Indies to Brazil; West Africa.

Remarks.—*Penaeus duorarum*, one of the western Atlantic littoral penaeids extensively utilized for food, is caught in commercial quantities throughout much of its geographic range (North Carolina to Nicaragua and perhaps Brazil (Lindner, 1957)). Distribution of this species is by no means uniform, consequently the fisheries are concentrated at diverse points, some of these being North Carolina, Key West, Fla., and Campeche Banks, Mexico, with the latter two being by far the largest. At other points in the range, the species is not abundant enough to support a fishery worthy of note.

A number of recent studies, especially in Florida, have greatly enhanced our knowledge of this species but only a brief summary is appropriate here.

In North Carolina, roe-bearing females and mature males appear in commercial catches from the ocean near Beaufort Inlet in May (Broad, 1950; Burkenroad, 1949; Williams, 1955a) and they continue to occur into July. Mature ovaries are blue-green in color. One spawning season a year is indicated for this, the northernmost breeding population of the species. There is strong evidence that this population is endemic.

In Florida, Cummings (1961) found stages of maturation in the ovaries of *P. duorarum* females similar to those in *P. setiferus*; i.e., the ovary passing through a flaccid undeveloped stage, a developing stage containing larger ova, a nearly ripe stage in which the ovary is large, visible from the outside and glaucous in color, and a ripe stage in which the ova contain characteristic rodlike refractive bodies, and finally a difficult-to-determine spent stage. The highest rate of spawning was judged to extend from April through July, a period comparable to that in North Carolina, but ripe and nearly ripe females were found at other times of year as well (see also Eldred, Ingle, Woodburn, Hutton, and Jones, 1961). Cummings indicated that multiple spawning probably occurs. Eldred, Ingle, Woodburn, Hutton, and Jones (1961) postulated that mating behavior is possibly

related to migratory behavior and that spawning is initiated at minimal bottom temperatures of 23.9° C. (see also Cummings, 1961). They suggested that annual temperature ranges within certain poorly understood, but not fatal, limits may have a controlling influence on population size in the following year.

The egg and larval stages of *P. duorarum* were described in detail by Dobkin (1961) from material taken from the Dry Tortugas fishing grounds. Viable, yellow brown, opaque eggs, 0.31–0.33 mm. in diameter, were obtained from mature females spawning in the laboratory. The act of hatching required 2 to 3 minutes. Dobkin described five naupliar, three protozoal, three mysis, and a number of postlarval stages. The naupliar and first protozoal stages were reared in aquaria, but remaining stages were taken from plankton.

Postlarvae of *P. duorarum* have been distinguished from those of *P. aztecus* by Williams (1959), and more fully described by Dobkin (1961). The recruitment period in North Carolina, extending from late May to November, agrees well with the occurrence of ripe adults in the fishery prior to and during the early part of this period, and it also suggests that movement and development time of larvae is about the same as that found in *P. setiferus* (i.e., 2 or 3 weeks). Bearden (1961) found a few postlarval *P. duorarum* from May through September in South Carolina.

Once on the nursery grounds in estuaries, the young undergo rapid growth. Williams (1955a) estimated an average increase in length of young shrimp at 52 mm. per month (about 1.8 mm. per day) for warmer months. More recent work shows that this estimate may be too high. Eldred, Ingle, Woodburn, Hutton, and Jones (1961) found that pink shrimp spawned in late March or April could reach lengths of 45–65 mm. by July, while those spawned in May could reach lengths of 25–35 mm. by July. Iversen and Jones (1961) showed that a 103-mm. shrimp will grow 7 mm., a 130-mm. shrimp will grow 5 mm., and a 153-mm. shrimp will grow little or none in a month in either summer or winter. Eldred, Ingle, Woodburn, Hutton, and Jones (1961) estimated that a 140-mm. shrimp is about 1 year old and that on such basis shrimp measuring 200 mm. in

length are approximately 2 years old. Most individuals that grow to maturity live a year or longer. Adult females attain a larger size than adult males (various authors).

The young shrimp tend to seek shallower, often somewhat fresher, portions of the estuaries in the early part of their benthonic existence, and with increasing size move gradually into deeper, saltier water as they grow; finally, with approaching maturity they return to sea. This general pattern of movement may best be taken as a model which is variously complicated in different parts of the species' range. In North Carolina, and perhaps elsewhere (Iversen and Idyll, 1960; Eldred, Ingle, Woodburn, Hutton, and Jones, 1961) many of the juveniles present in the sounds in fall do not return immediately to sea but linger in the estuaries over winter. Here they are often subjected to quite low temperatures (4° C.) and in severe winters nearly all of this overwintering population may be killed. Normally they survive the winter, but because they are relatively inactive in the cold, they grow little, at least in North Carolina (November–April estimated average increase in length, 7.5 mm. per month). Rising springtime temperatures induce increased activity and feeding, resulting in resumption of rapid growth and an ensuing spring migration to sea in May and June. In North Carolina, this migrating population is large enough to create a sizable late spring fishery.

In Texas (Hildebrand, 1955) and Florida (Higman, 1952) young of *P. duorarum* are especially abundant in grassy areas of estuaries where salinities are 20‰ or more. This is true of some areas in North Carolina, and the young are also concentrated most heavily in areas where there is a possibility of tidal transport (Williams, 1955b).

Tagging experiments to determine movements of this species have been restricted to waters off southern Florida. Iversen and Idyll (1960) and Iversen and Jones (1961) demonstrated a general northwestward movement for shrimp tagged on the fishing grounds west of Key West and suggested that small shrimp move from shallow water at the end of the Florida peninsula to the Tortugas fishing grounds.

Distribution of *P. duorarum* may be limited by the same factors that influence *P. setiferus*; i.e.,

salinity, temperature, and substrate. Hildebrand (1954, 1955) and Springer and Bullis (1954) emphasized the fact that *P. duorarum* fisheries are located in areas where the bottom is composed of calcareous muds and sands or mixtures of mud and sand. (This species usually burrows in the substrate in the daytime and is most active at night (various authors).) Laboratory experiments have shown that subadult *P. duorarum*, when allowed a free choice of sand, shell-sand, loose peat, muddy sand or sandy mud, tend to choose shell-sand with a somewhat lower preference for loose peat (Williams, 1958). In shell-sand the animals were often completely buried, and could be observed only after being dug out. The experiments confirmed observations on the correlation of location of fisheries with bottom type in the Gulf of Mexico and in North Carolina.

The fact that *P. duorarum* alone, of the three commercially abundant species of shrimps, is able to overwinter in estuaries in the northern part of its breeding range has suggested that it is better able to withstand a combination of low salinity and temperatures because of superior osmoregulatory abilities at low temperature. Preliminary studies have shown that *P. duorarum* is better able to regulate its internal fluids at low temperatures than its close relative *P. aztecus*, but regulatory ability of both species is impaired when temperatures are lowered to about 8° C., and survival of both species is better in moderate to high salinities at low temperatures (Williams, 1960). Eldred, Ingle, Woodburn, Hutton, and Jones (1961) considered that the depth to which the species may burrow in cold weather (6 inches) may protect it from sudden cold snaps.

Penaeus aztecus Ives. Brown or grooved shrimp

Figure 12

Penaeus brasiliensis aztecus Ives [in part], 1891, p. 190.
Penaeus brasiliensis: Hay and Shore [in part], 1918, p. 377.
Penaeus aztecus: Burkenroad, 1939, p. 34, figs. 20, 21, 24, 28–33 (rev.).

Recognition characters.—Integument thin, polished, translucent. Carapace with a median carina continuous anteriorly with rostrum and extending nearly to posterior border of carapace, flanked on each side by a broad, rounded groove; posterior half of carina with a median longitudinal groove; anterior half arcuate, highest above orbit and with 9 or 10 sharp teeth; pos-

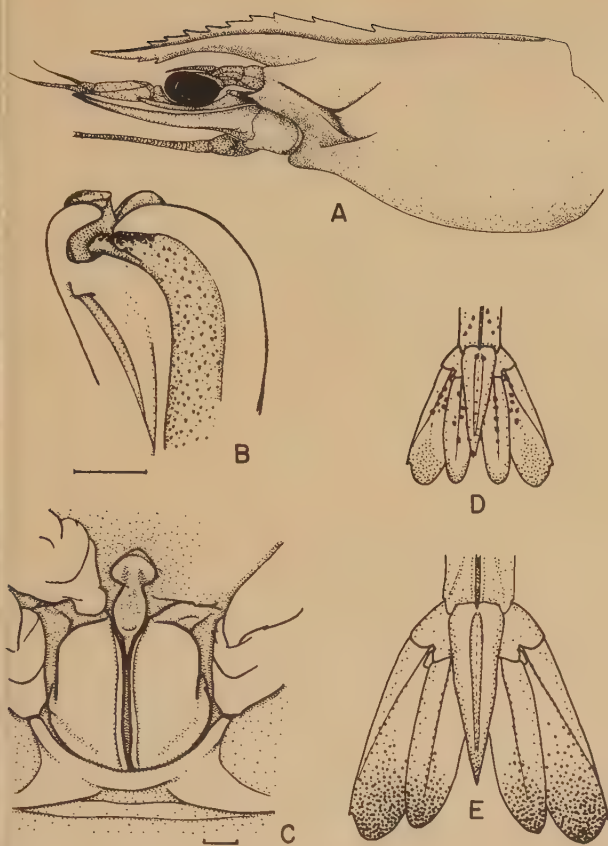


FIGURE 12.—*Penaeus aztecus* Ives. A, anterior portion of animal in lateral view, "Form A" from North Carolina, natural size; B, petasma of adult male, distal portion, view from right side; C, thelycum of adult female; B-C, 1 mm. indicated (after Burkenroad, 1939). Chromatophore distribution in tail fan (semidiagrammatic) of D, 17 mm. juvenile, E, 32 mm. juvenile; D-E, approximately $\times 5$ (after Williams, 1953).

terior tooth remote from others, anterior 6 or 7 on rostrum proper. Lower margin of rostrum with two or three teeth, tip slender, horizontal, or directed slightly upward, unarmed. Anterior margin of carapace with strong antennal spine on carina extending backward nearly to well-developed hepatic spine. Cervical groove extending halfway from hepatic spine to dorsal carina. A subhorizontal suture below hepatic spine, and a groove extending from near hepatic spine to near base of ocular peduncle. An orbital ridge behind eye.

Female with thelycum composed of two broad lateral plates and a median plate. Posteromedian part of median plate variably ovate-acuminate in

outline with tip raised into a short posterior carina diverging anteriorly into raised margins. Ventral surface concave; broad anterior end of posterior part merging into concave, triangular or semi-circular anterior portion. Lateral plates produced medially to meet in midline except diverging to expose median plate.

Abdomen with segments four to six carinate, carina of sixth flanked on each side by a narrow groove. Telson with deep median groove and an acuminate tip. Petasma of male with distoventral lobes not projecting free of distolateral lobes; with several compact series of short, crowded spines near distal ends; a fold of free margin of distolateral lobe beyond end of distoventral lobe bearing moderate spinose armature.

Measurements.—Length of body: large male, 162 mm.; large female, 211 mm.

Variations.—Burkenroad (1939) divided this species into "Forms," "A," "B," and "C." The chief differences are summarized here.

In "Form A," the grooves lateral to the dorsal carina are well defined posteriorly and are distinctly broader than the carina. The carina is distinctly and continuously grooved. The dorso-lateral grooves of the sixth abdominal segment are broadly open, their width "being from three-fourths to equal the interval between their dorsal lip and the midline."

In "Form B," the grooves lateral to the dorsal carina are usually much narrower than the carina and tend to be ill defined posteriorly. The dorso-lateral grooves of the sixth abdominal segment "range up to one-half as broad as the interval between their dorsal lip and the midline, and the dorsal lip is frequently low and ill defined."

In "Form C," the grooves lateral to the dorsal carina are much as in "Form A," but the carinal groove is shallow and frequently interrupted by plane intervals. The dorso-lateral grooves of the sixth abdominal segment are extremely narrow, "their width less than a third of the interval between their dorsal lip and the midline, and are sometimes entirely closed."

The rostrum is relatively shorter and deeper in old individuals than in young ones. In unworn adults, it reaches to or beyond the middle of the third antennular article. In young adults, it may reach the end of the antennal scale. The rostrum

in *P. aztecus* is more sinuous and slender than in *P. duorarum*.

Color.—Juveniles and young adults from estuaries or oceanic water near shore are usually brown or grayish brown, occasionally with darker spots or faint concentrations of chromatophores at the pleural articulations. Individuals from deeper water are light orange (Burkenroad, 1939). The tail fan is darkened distally and in adults is edged with purple to reddish purple. Detailed coloration of the young has been given by Williams (1953).

Habitat.—Estuarine and oceanic littoral, predominantly on mud bottom from water's edge to 45 fathoms; rarely to 89 fathoms.

Type locality.—Veracruz, Mexico.

Known range.—New Jersey (occasionally to Marthas Vineyard, Mass.) through Gulf of Mexico and West Indies to Uruguay.

"Form A," New Jersey to Campeche, Mexico.

"Form B," Florida through West Indies; Panama to Rio de Janeiro, Brazil.

"Form C," Pernambuco, Brazil, to Montevideo, Uruguay.

Remarks.—*Penaeus aztecus*, the third of the littoral penaeids abundant enough to be utilized profitably for food, is also fished commercially throughout much of its range (North Carolina to Brazil), and total landings for this species now outstrip the other two combined. When the U.S. Bureau of Fisheries began research on the natural history of *P. setiferus* in the 1930's, few grooved shrimp were sold, but with the advent of increased market, larger trawlers, and discovery of large concentrations of both *P. duorarum* and *P. aztecus* in different localities than had formerly been fished, the latter species were extensively utilized. Conversely, in recent years it is also possible that there has been a decline in abundance of *P. setiferus* throughout much of its range (various authors). Tremendous quantities of *P. aztecus* are now landed in the western Gulf of Mexico.

Prior to Burkenroad's revision (1939) of the grooved shrimps of the western Atlantic, three currently recognized species were lumped under the name *P. brasiliensis*. Biological data taken prior to that time on these species, never so extensive as those for *P. setiferus*, cannot now be assigned with certainty to any single species.

However, taking into consideration the locations where research was done, as well as modern knowledge of species distributions, it is probable that most of those data on grooved shrimps apply to *P. aztecus* (see also Pearson, 1939).

Maturation of gonads in *P. aztecus* probably parallels the process as understood in *P. setiferus*, although few data are recorded on this subject. Broad (1950) described maturing ovaries found in August as opaque white, yellow, tan, or gray in color. Burkenroad (1939), working in Louisiana, noted that whereas the proportion of males to females in *P. aztecus* near shore was about 1 to 1, this ratio progressively changed in samples farther from shore, in deeper water, to a ratio of 1 to 2 in water 50–70 fathoms deep. Moreover, the females in deep water were much larger than the males, a characteristic shown also by the related *P. setiferus* and *P. duorarum* and young adult populations of all three species inshore. Burkenroad attributed the size disparity of these large offshore individuals to greater length of life among females. Knowledge that impregnated females occurred only beyond 10 fathoms, together with the fact that mature (and possibly spent) ovaries were found only in individuals beyond these depths at various times of year, led him to propose that the females spawned a number of times during an ill-defined spawning season.

Williams (1959) favorably assessed Pearson's (1939) determination of *P. brasiliensis* (unfortunately misspelled "*brasiliensis*," in Williams) as most probably *P. aztecus*, and proceeding on the basis of Pearson's distinguishing characters was able to separate *P. duorarum* and *P. aztecus* postlarvae in the plankton in North Carolina. Postlarvae of the latter were found entering the sounds from October to May, with peak recruitment from late March to early April. Bearden (1961) found peak recruitment to occur in February and March in South Carolina. These patterns agreed well with collections of juveniles (Williams, 1955a) in which recruitment began in mid-April and continued through the summer. A long winter spawning season supplies postlarvae to the Carolina sounds, but fall and mid-winter recruits are apparently killed by cold weather for they never progress beyond postlarvae

in the samples taken. Pearson found postlarvae in Louisiana in all months of the year, but in no more than 11 months of any calendar year. The usual recruitment period seemed to run from late January to late summer.

Gunter (1950) found young brown shrimp in Texas bays most common in spring and fall with low abundance in late summer and winter.

Evidence indicates that *P. aztecus* has an extended spawning season which probably varies in different parts of the range. The spawning site is probably deeper and farther from shore than in *P. setiferus* and *P. duorarum*.

Young *P. aztecus* enter estuaries as postlarvae, migrate to shallow, often low-salinity water, and undergo a remarkably rapid growth in the warmer months. In North Carolina, the juveniles increase in mean length by an estimated 46 mm. per month (1.5 mm. per day, Williams, 1955a). As they grow, they gradually move to deeper, saltier water and eventually return to sea. In North Carolina, and perhaps elsewhere, *P. duorarum* and *P. aztecus* use essentially the same nursery grounds over large areas of the sounds; however, the seasons of recruitment to and occupation of these areas is staggered in such a manner that the two species are rarely on common ground (Williams, 1955a, b). The growing bait fisheries for estuarine shrimp in recent years have given impetus to studies in Alabama and Texas. Additional information on migration (Loesch, 1957) and studies on length-weight relationships (Chin, 1960) have resulted from this work.

Again, distribution of *P. aztecus* is usually thought of as limited by such factors as salinity, temperature, and substrate. Hildebrand (1954, 1955) and Springer and Bullis (1954) stated that the commercial fishery for this species in the Gulf of Mexico was confined largely to bottoms of terrigenous silt. (Like *P. duorarum*, *P. aztecus* is a burrower, and in many areas is more active in open water at night than in daytime.) In experimental tanks, when given a choice of sand, shell-sand, loose peat, muddy sand and sandy mud, *P. aztecus* was found to favor loose peat, sandy mud and muddy sand, closely paralleling *P. setiferus* in choice of bottom type (Williams, 1958). The experiments confirm field ob-

servations on habitat along the coast of North Carolina and in the Gulf of Mexico.

Penaeus aztecus has been found to have a less efficient osmoregulatory mechanism at low temperatures in low salinities than *P. duorarum* (Williams, 1960). For this reason, it is probably not so resistant to wintertime conditions in estuaries as *P. duorarum*.

Genus *Parapenaeus* Smith, 1886

Burkenroad, 1934b, p. 107.

Parapenaeus longirostris (Lucas)

Figures 13-15

Penaeus longirostris Lucas, 1849, p. 46, pl. 4, fig. 6.

Parapenaeus politus: Hay and Shore, 1918, p. 379, pl. 25, fig. 7.

Parapenaeus longirostris: Burkenroad, 1934b, p. 108 (rev.).—1939, p. 53.

Recognition characters.—Integument smooth, not setose. Carapace with a low carina extending almost to posterior margin and bearing a spine some distance behind rostrum. Rostrum arched; distal half deflexed, tip somewhat upturned, extending to or beyond distal edge of eye; dorsal margin with usually seven teeth diminishing in size anteriorly; ventral margin heavily ciliated. Hepatic, antennal, and branchiostegal spines well developed; later spine placed a little behind margin of carapace. A rectangular toothlike eminence at orbital angle. A shallow groove extending from behind eye almost to posterior edge of carapace, and another, extremely faint, running upward from inferior margin at base of second pair of legs. Basal antennular article with a spine on ventromedian margin distally.

Thelycum of female composed externally of a triangular plate with obtuse apex on 13th somite (base of 4th leg); 14th sternite raised anteriorly, with low relief posteriorly; lateral ridges with nearly straight but divergent medial borders separated by nearly plane, broad medial groove; lateral border of ridges ornately curved to fit contour of adjacent coxae and 13th sternite.

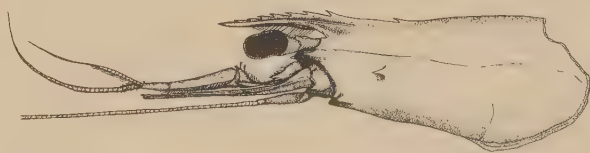


FIGURE 13.—*Parapenaeus longirostris* (Lucas). Anterior portion of animal in lateral view, $\times 3$.

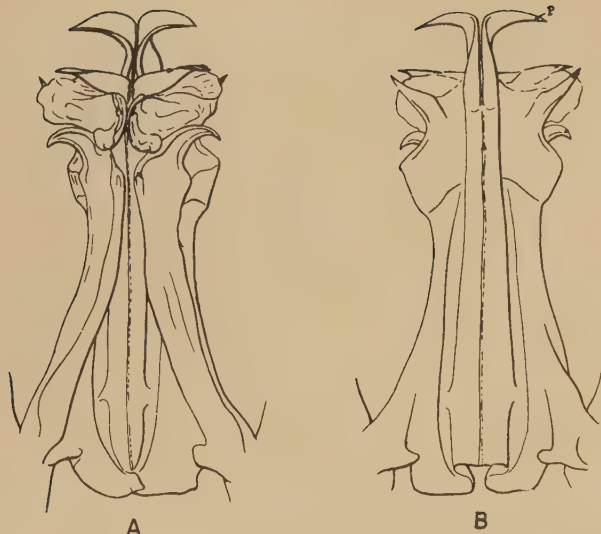


FIGURE 14.—*Parapenaeus longirostris* (Lucas). Petasma of male, A, ventral view; B, sternal view (after Heldt, 1938).



FIGURE 15.—*Parapenaeus longirostris* (Lucas). Thelycum of female; A, external plate of somite 13; B, internal structure showing sacs extending into somite 14 (after Heldt, 1938).

Petasma of male with each half terminating in a dorsomedian spinelike projection with a fleshy distomedian lobe at base; proximal to latter, a broad lateral spine with a fleshy distolateral lobe at base continuous with distomedian lobe but not projected laterally as a spoutlike horn as in *Xiphopenaeus*; finally, still further proximally a spinelike distoventral projection partially covered by a medial distoventral flap.

Abdomen with fourth, fifth, and sixth segments carinate, carina ending on each segment in a small tooth. Sixth segment a little more than twice length of fifth. Telson tapering to a sharp point, furrowed above, with a slender spine on each side near tip.

Measurements.—Western Atlantic population: length of body, 104 mm. Mediterranean population: length of body, 165 mm.

Variations.—European examples of the species attain a greater size than do American forms. The length of the rostrum varies with age, becoming relatively longer with variable development of an unarmed tip in large individuals. The sixth abdominal segment is relatively shorter in large than in small individuals.

Color.—Eyes green; body and appendages mottled with red and pale translucent areas; uropods with exopod and distal half of endopod deep red (Burkenroad, 1934b).

Habitat.—Soft mud or muddy sand bottom (Heldt, 1954); 15 to 180 fathoms or more in western Atlantic (Burkenroad, 1934b, 1939); 20 to 250 fathoms in Mediterranean (Heldt, 1954, 1955).

Type locality.—Algiers and Cap-Matifou, Algeria.

Known range.—Marthas Vineyard, Mass., to Gulf of Mexico off Florida, Louisiana, and Yucatan; Gulf of Paria off Venezuela; coast of Portugal to Morocco; Mediterranean Sea from Spain to Asia Minor.

Remarks.—Though this species occurs on both sides of the Atlantic, it has been studied in detail chiefly in the European portion of its range. The European population is composed of larger individuals than the American population (Burkenroad, 1934b) and because of its size and abundance is commercially exploited off the coast of Tunisia (Heldt, 1954). The American population is also quite abundant in the northern Gulf of Mexico (Burkenroad, 1939).

It is possible that this species lives beyond the 100-fathom depth off the Carolinas, but because it is known to move into shallower water in parts of its range it is included here. Heldt (1938) stated that the depth distribution starts at about 30 fathoms, but usually extends from 55 to 200 and more fathoms. She described characteristic features of what she termed the "fonds à *Parapenaeus*" in the Mediterranean Sea (1954).

The developmental stages of this species have been treated in detail by Heldt (1938) from the Mediterranean and in somewhat lesser detail by Pearson (1939) from the northern Gulf of Mexico.

Heldt described cleavage stages of the egg, formation of the embryo, 8 naupliar, 3 protozoal, 14 mysis stages, and the first postlarval stage. Pearson found protozoal, mysis, and postlarval stages principally during July off South West Pass, La.; and usually a complete set of larval stages was taken in a single plankton collection. A single mysis was taken south of Barataria Pass, La., in May and a single first protozoa at Fort Pierce, Fla., in January.

Genus *Penaeopsis* Bate, 1881

Bate, 1881, p. 182.

Penaeopsis goodei (Smith)

Figures 16-17

Parapenaeus goodei Smith, 1885, p. 176.

Penaeopsis goodei: Verrill, 1922, p. 44, pl. 15, figs. 1A-1Aiv; pl. 16, fig. 3.—Burkenroad, 1934a, p. 15, figs. 2, 3 (rev.).

Recognition characters.—Carapace and abdomen covered with rather stiff, plumose hairs. Carapace about as wide as deep and very little compressed anteriorly. Rostrum rising obliquely above level of dorsum, shorter than carapace proper and armed above with 8 to 10 teeth in front of orbital margin; a sharp gastric tooth behind rostral carina. Antennal, hepatic, and branchiostegal spines well developed; a rectangular toothlike eminence at orbital angle; grooves inconspicuous. Eyes large, reniform, flattened above. Antennular flagella subequal in length and about as long as second article of peduncle. Antennal scale reaching to tip of antennular peduncle; distal portion of thickened outer margin armed above with series of minute spines directed obliquely forward and outward.

Third maxilliped, first and second legs armed with basal spines. A small distal spine on ventral side of ischium of first leg. A pair of long, slender spines arising from sternum between second legs.

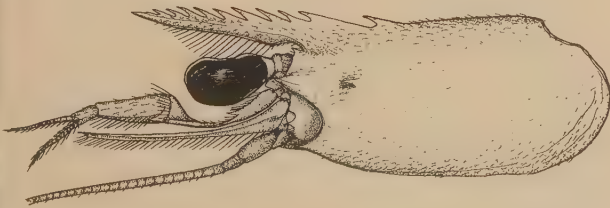


FIGURE 16.—*Penaeopsis goodei* (Smith). Anterior portion of animal in lateral view.



FIGURE 17.—*Penaeopsis goodei* (Smith). A, petasma of male in ventral view, approximately $\times 9.5$; B, petasma in ventral view, distal portion with right external piece removed, approximately $\times 14$ (after Burkenroad, 1934a).

Thelycum of female composed of an anterior flattened oval portion with a slender anterior median spine on 13th somite (between 4th leg), and a short broad, posterior portion on 14th somite connected to preceding structure by a less elevated median prominence flanked by an irregular bulbous enlargement on each side. Petasma of male exceedingly complicated and asymmetrical; left side irregularly folded longitudinally, projecting proximally in a curved process beyond right half and to right of median line, and extending distally in an irregular process; right side enlarged distally and divided into several irregularly curved processes projecting beyond left appendage, and partially covered posteriorly by a thin spoon-shaped lamella arising at their bases.

Abdomen with third to sixth segments carinate dorsally; carina of fourth and fifth narrowly cleft at posterior margin. Telson considerably longer than sixth segment; rounded and obscurely grooved above; regularly tapered; armed with a long spiniform process at each side of acute tip, and three pairs of movably articulated spines in front of lateral spines, posterior ones largest.

Measurements.—Length of carapace including rostrum: male, 19 mm.; female, 21 mm.

Habitat.—Surface to 180 fathoms.

Type locality.—Bermuda.

Known range.—Between Capes Hatteras and Lookout, N.C., through Caribbean Sea and West Indies to Surinam; Bermuda.

Remarks.—Larval stages from Bermuda that probably belong to this species were described by Gurney (1943b). From observations at Bermuda, Wheeler (1937) described characteristic swarming of this species at about an hour after sunset, with monthly maxima on the 2d and 26th days of the lunar month.

Genus *Xiphopeneus* Smith, 1869

Burkenroad, 1934b, p. 102.

Xiphopeneus kroyeri (Heller)

Figures 18–20

Peneus kroyeri Heller, 1862, p. 425, fig. 51.

Xiphopeneus kroyeri: Burkenroad, 1934b, p. 103, fig. 12 (rev.).—Schmitt, 1935a, p. 132, fig. 5.—Holthuis, 1959, p. 70, fig. 7.

Recognition characters.—Carapace and abdomen smooth. Rostrum laterally compressed, sinuous, armed with usually five dorsal teeth at base, styliform tip greatly elongated beyond antennal scales and varyingly elevated. Carapace with a single epigastric tooth behind rostral series on rounded postrostral carina extending from base of rostrum to near posterior border; no transverse suture in adults; anterior cervical groove reaching anterior margin and continuous with branchiocardiac groove reaching almost to posterior border; hepatic and antennal spines present. Antennal flagella much longer than body; antennal scale extending beyond tip of antennular peduncle. Inferior antennular flagellum up to 50 percent length of antenna. Exopodites of second and third maxillipeds slender.

Last two pairs of legs elongate, flagelliform, with dactyls many jointed.

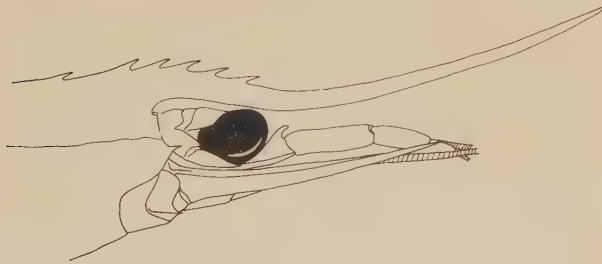


FIGURE 18.—*Xiphopeneus kroyeri* (Heller). Anterior part of animal in lateral view, approximately $\times 3.2$ after Holthuis, 1959).

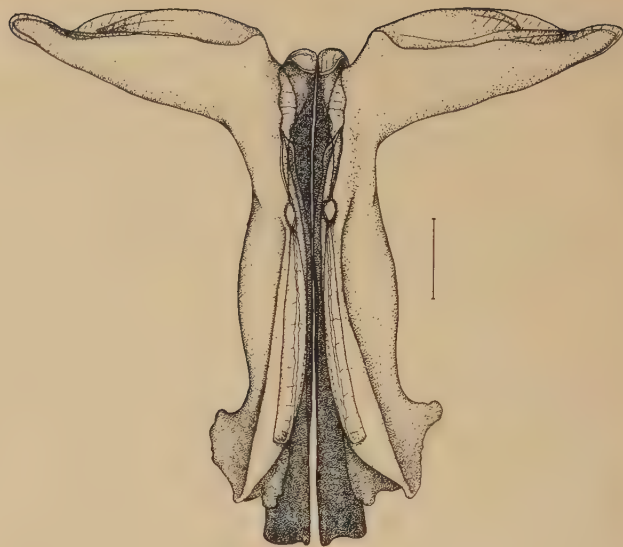


FIGURE 19.—*Xiphopeneus kroyeri* (Heller). Petasma of adult male, ventral view, 1 mm. indicated.



FIGURE 20.—*Xiphopeneus kroyeri* (Heller). Thelycum of female, filled sperm sacs showing through abdominal integument (after Burkenroad, 1934b).

Fourth to sixth abdominal segments carinate, with small dorsal tooth at posterior end of carina on each segment; sixth segment with carina high and deep. Telson tapering to acute tip.

Petasma of male with distolateral corners greatly produced as hornlike projections, open along distal margins on thoracic face. Thelycum of female externally appearing as an unpaired plate extending forward from last thoracic somite.

Measurements.—Length of body: 127 mm.

Variations.—The rostrum is somewhat longer in females than in males, and varies with age. In individuals with carapace length under 9 mm., the rostrum is shorter than the carapace, but beyond this size it is usually longer than the carapace.

Color.—Whitish, ventral part yellowish, occasionally with yellow over whole body but most

distinct ventrally; dark chromatophores scattered throughout and when expanded giving animal a grayish cast; tips of rostrum and flagella reddish; legs pinkish or yellowish orange; pleopods and uropods yellowish at base, pink distally; telson and sixth abdominal segment sometimes pink (Holthuis, 1959).

Habitat.—This species lives in a narrow zone along shore, and at times in the lower portion of estuaries (Gunter, 1950; Holthuis, 1959), from 2.5 to 20 fathoms, rarely to 24 fathoms (Burkenroad, 1939; Gunter, 1950).

Type locality.—Rio de Janeiro, Brazil.

Known range.—Between Capes Hatteras and Lookout, N.C., through Gulf of Mexico and Caribbean Sea to near Santos, São Paulo, Brazil; Pacific coast variety (*X. riveti*, see Burkenroad, 1934b) from Mexico to northern Peru.

Remarks.—This species is of commercial importance in the southern United States (Weymouth, Lindner, and Anderson, 1933; Hildebrand, 1954), and of great importance in South America (Lindner, 1957; Higman, 1959), especially along the northeast coast where it dominates the near-shore fishery and the young dominate the coastal nursery areas, perhaps offering serious competition to other penaeids.

No detailed study of the ecology of this species has been made. Burkenroad (1949) observed ripe or nearly ripe females off North Carolina in May, and Gunter (1950) found them along the Texas coast in June. Vieira (1947), in a study on maturation, found mature females off São Paulo, Brazil, from November to January.

Gunter (1950) studied a population ranging in size from 28 to 127 mm. total length. He found a population mode of 38 mm. total length in October but no definite modes in other months. The species was most abundant in fall. Gunter pointed out that the species does not customarily live in bays, even though it lives in shallow water close to the Texas shore. The young may enter the lower end of Texas bays (21.2–30.7 ‰), but most individuals were found in the Gulf of Mexico in a salinity range of 29.7 to 35.2 ‰. Similar salinity tolerances were implied by Lindner (1957) and noted by Holthuis (1959). Though the South American shrimp are caught in estuaries and rivers, the penetration into these areas is greatest in dry seasons. Both Lindner

and Holthuis gave data on the fisheries and processing methods.

Genus *Trachypeneus* Alcock, 1901

Burkenroad, 1934b, p. 94.

Trachypeneus constrictus (Stimpson)

Figure 21

Penaeus constrictus Stimpson, 1871b, p. 135.

Trachypeneus constrictus: Hay and Shore, 1918, p. 378, pl. 25, fig. 9.—Schmitt, 1935a, p. 131.

Recognition characters.—Dorsal region of carapace with fine, short, appressed setae; branchial region of carapace and last two abdominal segments variably pubescent; abdomen smooth proximally. Carapace carinate except for short stretch near posterior border; a spine behind base of rostrum; antennal and hepatic spines well developed; a rectangular toothlike eminence at orbital angle; lateral groove extending about three-fifths length of carapace; anterolateral angle truncate. Rostrum reaching to about middle of second segment of antennal peduncle, directed slightly upward; upper margin usually slightly arched and bearing usually seven to nine equidistant teeth diminishing in size toward tip. Eyes large, reniform. Antennular peduncle pubescent above, extending slightly beyond antennal scale; flagella shorter than carapace. Third maxilliped, first and second legs with basal spines.

Abdomen carinate from fourth to sixth segment. Telson with two rounded carinae above; tapering to a short acuminate tip, armed on either side with a short spine.

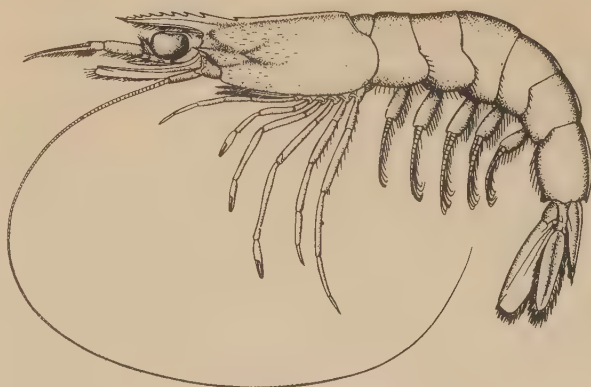


FIGURE 21.—*Trachypeneus constrictus* (Stimpson). Animal in lateral view, approximately $\times 1.5$ (after Verrill, 1922).

Thelycum of female with anterior margin of median plate and lips of transverse groove evenly rounded, notched in middle; lateral flaps of last thoracic somite overlapping median plate; rib supporting expanded median plate extending anteriorly and sharply set off from anterior ventral margin of plate; ventral surfaces pubescent. Sternal elevation between coxae of fifth leg of male with lateral margins indented setting off posterior portion from broad anterior basal portion; petasma with distolateral corners greatly produced as hornlike projections.

Measurements.—Length of body: 92 mm.

Color.—Translucent with purplish-gray blotches; appendages pink.

Habitat.—Primarily sand or mud and shell bottom in high-salinity water; shallow water to 30 fathoms.

Type locality.—Beaufort, N.C.

Known range.—Tangier Sound, Chesapeake Bay, to Texas; Bermuda; Puerto Rico and Sombrero Island; Surinam.

Remarks.—Eldred (1959) reported *T. constrictus* as common in the Tortugas area of Florida where, along with its near relative, *T. similis*, it makes up about 7 percent of the annual commercial catch. It probably contributes more to catches in deeper water than to catches in the area sampled. Gunter (1950) stated that *T. constrictus* was rarely taken in coastal bays of Texas, being largely confined to water above 30‰. In littoral waters, ripe females were taken in September and small specimens (about 29 mm. total length) in March.

Burkenroad (1939) remarked that *T. constrictus* might be restricted largely to sandy bottom, and Hildebrand (1955) suggested a distribution possibly correlated with bottom type, but did not specify the type.

The early developmental stages of *T. constrictus* were treated by Pearson (1939). All larval and postlarval stages were pieced together by successful rearing techniques coupled with plankton catches at St. Augustine Inlet, Fla. Descriptions were given of the egg (from the two-cell stage onward), five naupliar, three protozoal, two mysis, and early postlarval stages. A year-round spawning season is indicated, because eggs were taken at St. Augustine, Fla., from April to August, and at Fort Pierce, Fla., in summer and

from December to February. Nauplii were found from April to August, and the remaining stages from May to August, with a few protozoae being taken also in winter. Pearson found developmental stages of this species more abundant than those of related species in shallow oceanic water; in estuarine water the postlarvae were rare. He attributed this rarity and the comparative scarcity of adults in commercial catches to the burrowing habits of postlarvae and adults, as observed in the laboratory. Somewhat contrary to Pearson's findings, the juvenile stages of this species have been caught commonly in surface plankton tows made with a coarse-mesh net on nightly flood tides in Bogue Sound near Beaufort Inlet, N.C. These collections have been made in summer and fall (mid-June to mid-November) when salinities ranged from 28 to 36 ‰.

Subfamily Sicyoninae

Body more or less sculptured and rigid, with prominent, often more or less interrupted dorsal carina. Carapace with or without spine at antennal angle. Lateral section of ocular somite developed into elongated stylet. Basal antennular article lacking enlarged ciliated protuberance (prosartema) on inner proximal margin. No pleurobranchs behind ninth somite (third maxilliped). Fourteenth somite (fifth legs) without gills. Pleopods lacking endopods except in modified form on first and second pleopods of male (modified after Burkenroad, 1934b).

Burkenroad (1934b) pointed out that the subfamily Sicyoninae is an extremely uniform group. Unlike other penaeids, sexual maturity may be attained at a quite small size. "Differences between small and large individuals of any species are slight and chiefly affect rostral length, elevation and distal armature, these features in general becoming respectively shorter, more horizontal, and with more numerous distal teeth as size increases, and the armature of the pleonic [abdominal] pleura, which generally increases in strength and extent with growth." The thelycum, and corresponding male genital sternites, are less varied than among other penaeid groups, and, consequently, are not so serviceable in distinguishing species. The serious student is referred to Burkenroad (1934b, pp. 70-76) for full discussion of these characters.

Genus *Sicyonia* Milne Edwards, 1830

Burkenroad, 1934a, p. 70.—1945, p. 1.—Hall, 1956, p. 87.—Hemming, 1958b, p. 126.

The generic name *Sicyonia* has had a complex nomenclatural history, and was reviewed in detail

by Burkenroad (1945) and Hall (1956). The name *Sicyonia* H. Milne Edwards, 1830, has been validated under Plenary Powers of the International Commission on Zoological Nomenclature (Opinion 382; Hemming, 1958b).

KEY TO SPECIES IN THE CAROLINAS

(Modified after Lunz, 1945)

- a. Antennal angle not armed with a definite spine; ischium of first leg armed with a spine.
 - b. Rostrum (excluding tip) with two dorsal teeth before posterior margin of orbit; carina of carapace with three teeth, first tooth smallest.....*laevigata* (p. 33).
 - bb. Rostrum (excluding tip) with three dorsal teeth; carina of carapace with three evenly spaced, subequal teeth.....*parri* (p. 34).
- aa. Antennal angle armed with definite spine (sometimes blunt); ischium of first leg unarmed.
 - b. Three or four teeth on carina of carapace behind orbital margin, three large; carina high; rostrum extending beyond midpoint of cornea, with two dorsal teeth (excluding tip).....*brevirostris* (p. 35).
 - bb. Two or three teeth on carina of carapace behind orbital margin, two large and behind hepatic spine; rostrum not extending beyond midpoint of cornea, with one or two dorsal teeth (excluding tip).....*typica* (p. 36).
 - bbb. Two teeth on carina of carapace behind orbital margin, one behind hepatic spine; rostrum with three dorsal teeth (excluding tip).
 - c. Fourth abdominal segment with anterior and posterior ends of ventral margin of pleura spined or angular.....*dorsalis* (p. 37).
 - cc. Fourth abdominal segment with posterior end of ventral margin of pleura rounded.....*stimpsoni* (p. 38).

Sicyonia laevigata Stimpson

Figures 22–23

Sicyonia laevigata Stimpson, 1871b, p. 131.—Hay and Shore, 1918, p. 379, pl. 25, fig. 1.

Eusicyonia laevigata: Burkenroad, 1934a, p. 76, figs. 21, 26, 32 (rev.).—Lunz, 1945, p. 4, fig. 1.

Recognition characters.—Integument rather firm, finely granulate and more or less sculptured. Rostrum elevated at angle of about 20 degrees, about half as long as carapace; armed dorsally with two teeth not counting tip; terminal portion divided into four teeth; notch between median pair shallower than dorsal and ventral notches; often two short, stout, asymmetrically placed, mobile spines distally above ventral margin. Postrostral carina with three teeth behind orbital margin; anterior one slightly advanced beyond level of hepatic spine and about same size as rostral teeth, often appearing as part of rostral series; posterior two teeth closer together; carina sometimes nearly obliterated anterior to each tooth. Antennal angle unarmed but not rounded. Ocular stylets short.

Abdominal segments marked by tergal carinae deeply notched behind on first to fifth segments. First abdominal segment with carina produced into an elevated anterior tooth; marked laterally by two grooves, a long posteromedian and short anteromedian groove obliterated a short distance

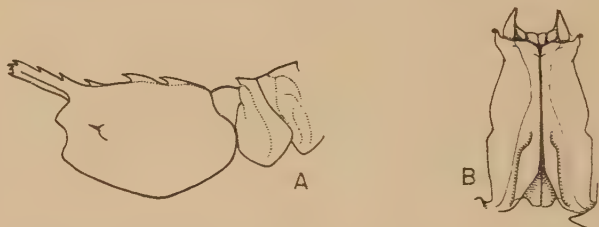


FIGURE 22.—*Sicyonia laevigata* Stimpson. A, carapace and first two abdominal segments in lateral view, approximately $\times 3$; B, petasma of male in ventral view, approximately $\times 20.5$ (A–B after Burkenroad, 1934a).

ventral to juncture with anterior margin of pleura but with short resumption below juncture. Second and third segments with anterior and short posterior tergal grooves; a short, shallow anteromedian pleural and a posteromedian pleural groove turning sharply anteriad somewhat above middle of lateral surface. Second segment with carina narrowly and deeply cleft above juncture of tergal groove. Fourth and fifth segments with posterior tergal groove, and an anterior groove, obliterated for interval below short dorsal section; reappearing farther ventrad. Sixth segment with a posteromedian pleural, anterior tergal and a longitudinal groove; carina ending in a strong posterior tooth. Ventral pleural margins rounded except for a posterior tooth on fifth and sixth segments.

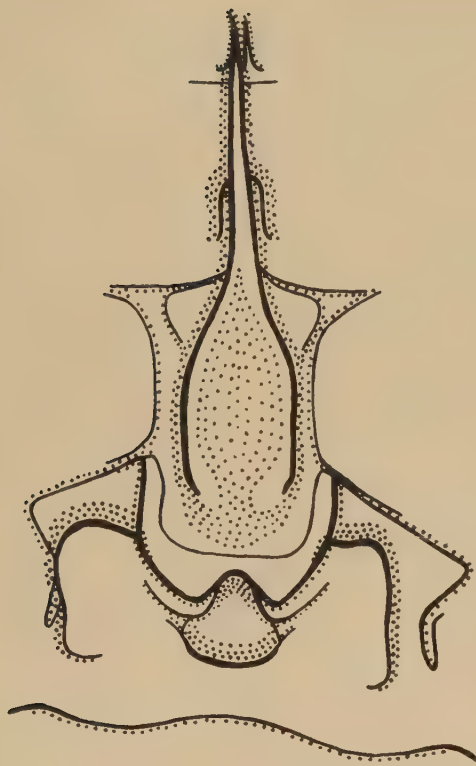


FIGURE 23.—*Sicyonia laevigata* Stimpson.
Thelycum of female, $\times 10.4$ (after Burkenroad, 1934a).

Telson ending in a strong point flanked by a pair of shorter blunt spines; sometimes with a pair of mobile lateral spines distal to basal shoulders.

Petasma of male with distolateral projections extending straight distally. Thelycum most conspicuously marked by elongate plate arising on 13th somite (between 4th legs), with slender tip extending to level of 11th somite (2d legs).

Measurements.—Length of body: males, 14 mm.; females, 50 mm.

Variations.—The angle of elevation of the rostrum varies with age. Nearly horizontal among the young, it rises to as much as 35 degrees in older individuals. The usual angle is somewhat in excess of 20 degrees. The number of carinal teeth on the carapace may be reduced to two (Lunz, 1945).

Color.—Yellowish brown; carapace darker than abdomen and sometimes bluish or greenish.

Habitat.—A littoral species fairly common in the Carolinas, especially on shelly bottoms of harbors; shallow water to 49 fathoms.

Type locality.—Charleston, S.C.

Known range.—Cape Hatteras, N.C., to northwest Florida; through West Indies to Colombia; Pacific coast of Panama.

Remarks.—This small species becomes sexually mature at quite a small size (length of 18 mm.).

Sicyonia parri (Burkenroad)

Figure 24

Eusicyonia parri Burkenroad, 1934a, p. 80, fig. 22.—Lunz, 1945, p. 5, fig. 2.

Recognition characters.—Resembling *S. laevigata*; integument rather firm, almost smooth and more or less sculptured. Rostrum elevated at angle of about 15 degrees, armed dorsally with three teeth not counting tip; terminal portion bearing three teeth with rudiment of another between lower teeth. Postrostral carina armed with three large, subequal teeth, anterior one slightly advanced beyond level of hepatic spine.

Abdominal segments marked by tergal carinae notched behind on first to fifth segments. First abdominal segment with carina produced into an elevated anterior tooth, marked laterally with a short anteromedian groove as in *S. laevigata*, but reappearing below obliteration and continuing conspicuously to ventral margin, not connected to posteromedian pleural groove ventrally. Second segment with carina cleft above juncture of tergal grooves. First four segments each with a shallow but perceptible posterior pleural groove. Fourth segment with dorsal and ventral positions of anterior tergal groove separated by narrow area of obliteration.

Petasma of male with distolateral projections curved medially at tips; distoventral lobes constricted abruptly near tip.

Measurements.—Length of body: female, 25 mm.

Habitat.—Shallow water to 14 fathoms.

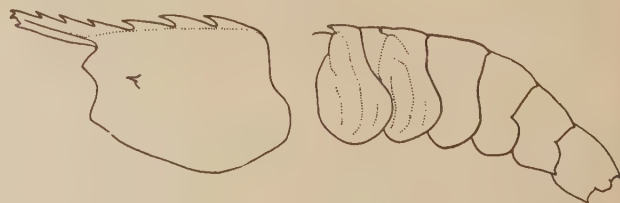


FIGURE 24.—*Sicyonia parri* (Burkenroad). Carapace and abdomen in lateral view, approximately $\times 3$ (after Burkenroad, 1934a).

Type locality.—Crooked Island, Bahamas.

Known range.—Beaufort, N.C.; Florida; West Indies to Curaçao.

Sicyonia brevirostris Stimpson

Figures 25–26

Sicyonia brevirostris Stimpson, 1871b, p. 132.—Hay and Shore, 1918, p. 380, pl. 25, figs. 2, 4.

Eusicyonia brevirostris: Burkenroad, 1934a, p. 84 (rev.).—Lunz, 1945, p. 6, fig. 3.

Recognition characters.—Integument firm, much sculptured, especially abdomen; abdomen with scattered tubercles, and whole body with covering of short, fine hairs. Rostrum short, elevated, slender, narrowing considerably to tip; extending beyond midpoint of cornea; armed dorsally with two (occasionally three) teeth not counting tip; terminal portion divided into two or three teeth with ventral tooth projecting distally farther than dorsal tooth. High postrostral carina with three or four teeth behind orbital margin. Antennal angle armed with a small spine. Hepatic spine well developed. Ocular stylets long.

Abdominal segments marked by prominent tergal carinae deeply notched behind on first to fifth segments. First abdominal segment with carina produced into an elevated anterior tooth; marked laterally by four grooves, an antero-median and posteromedian pleural, a posterior pleural and posterior tergal. Second and third segments grooved with two tergals, two median pleurals extending far dorsad, and a posterior pleural. Fourth segment grooved with two tergals and one pleural; fifth with two tergals. Sixth segment with a posteromedian pleural, anterior tergal, and a longitudinal groove. Fifth and sixth segments each with carinal tooth directed posteriorly. Pleura of first four segments armed with an anterior ventral angle; angle produced



FIGURE 25.—*Sicyonia brevirostris* Stimpson. Carapace and first two abdominal segments in lateral view, 5 mm. indicated (after Lunz, 1945).

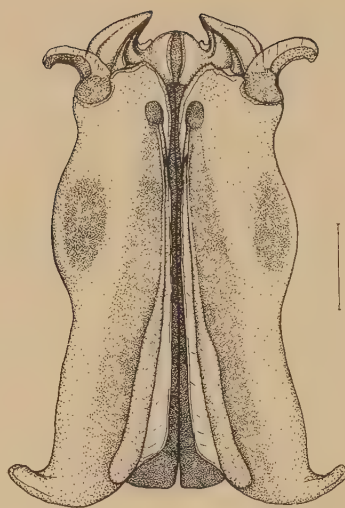


FIGURE 26.—*Sicyonia brevirostris* Stimpson. Petasma of adult male, ventral view, 1 mm. indicated.

into blunt, outward pointing spine on third and fourth, sometimes also on second segment. Last three segments armed with posterior ventral tooth. Telson ending in a strong point flanked by a shorter pair of subterminal, often obsolescent, spines.

Petasma of male with distolateral lobes curved medially, distoventral lobes curved laterally.

Measurements.—Length of body: males and females 153 mm.

Variations.—This species exhibits considerable variation in degree of elevation of the rostrum (5–45 degrees). The rostral length also varies, and length and angle of elevation tend to decrease with increasing age, but this tendency is highly irregular.

Considerable variation in placement of teeth on the carapace occurs. The anterior tooth of the dorsal carina may be located behind the orbital margin and appear as part of the carapace series, in which case there are four teeth on the carapace and two on the rostrum (exclusive of tip); or, this tooth may be located anterior to the orbital margin and appear as part of the rostral series, in which case there are three teeth on the rostrum and three on the carapace.

Color.—Ground color off white to light pink, pubescence grayish to grayish yellow; dorsal carina barred with white; appendages reddish

purple, thoracic appendages barred with white; ventral side of abdomen and uropods reddish, sternal ridges white with purple tipped median spines. Burkenroad (1939) gave a somewhat different and more detailed color description.

Habitat.—Common in offshore littoral of the Carolinas; on white shell sand on Campeche Banks; shallow water to over 100 fathoms in Carolinas (Broad, 1950), rarely to 180 fathoms.

Type locality.—Cuba.

Known range.—Off Norfolk, Va., through Bahamas and Gulf of Mexico to Yucatan, Mexico; Pacific coast of southern Mexico.

Remarks.—This large sicyonine shrimp is fairly common in North Carolina and has had a limited commercial usage. Formerly thought to be rare in South Carolina (Lunz, 1945), it is now found to be widely distributed out to the 50-fathom curve (Lunz, 1957). Eldred (1959) reported few *S. brevirostris* in the Tortugas controlled area off Florida. Hildebrand (1954) found the species to be fairly abundant on the Campeche fishing grounds where the bottom is white shell sand. On the Texas brown shrimp grounds and Campeche Banks, the species is rare in depths of 15–25 fathoms where *S. dorsalis* predominates on mud bottom. In deeper water and on mud bottom, 31–45 fathoms, it is more abundant. It is also common in shallow water at 6–10 fathoms. Hildebrand suggested a distribution in two zones separated by an intermediate zone where *S. dorsalis* predominates, or possibly the deeper zone of *S. brevirostris* over mud represents strays. On Campeche Banks, *S. brevirostris*, *dorsalis*, and *typica* have been taken together.

Lunz (1957) reported natural history notes on *S. brevirostris* in South Carolina based on 169 successful 30-minute hauls with a 20-foot experimental trawl. He found the species most abundant in depths of 35–40 fathoms. Catches at night were larger than those made in daytime. Though available throughout the year, largest catches were made in December. Meager data on maturity of gonads indicated spring and fall spawning seasons.

Sicyonia typica (Boeck)

Figure 27

Sicyonia carinata Milne Edwards, 1830, p. 344, pl. 9, fig. 9.—Bate, 1888, p. 294, pl. 43, figs. 2–3.

Synhimantites typica Boeck, 1864, p. 189.—Danielssen and Boeck, 1872, p. 192, figs. 1–14.—Sars, 1883, pp. 8, 49.

Sicyonia edwardsii Miers, 1881, p. 367.—Milne Edwards and Bouvier, 1909, p. 251, pl. 8, figs. 1–3 (not fig. 4) (rev.).—Hay and Shore, 1918, p. 380. Schmitt, 1935a, p. 133 (not fig. 6).—Lunz, 1945, p. 7, fig. 4.

Sicyonia typica: Burkenroad, 1945, p. 2 (rev.).—Holthuis, 1959, p. 77.

Recognition characters.—Integument rather firm, more or less sculptured and covered with a short, thick pubescence more evident dorsally than ventrally, especially on abdomen. Rostrum extending halfway along eye, directed obliquely upward, armed dorsally with one or two small teeth not counting tip. Postrostral carina with two or three teeth, last two placed behind level of hepatic spine (third tooth, if present, may look like part of rostral series). Antennal angle armed with a short, often blunt, tooth.

Abdominal segments marked by tergal carinae deeply notched behind on first to fifth segments; first segment with carina produced into an elevated anterior tooth; fifth segment with carina ending posteriorly in a low tooth; sixth segment with carina produced into a posteriorly directed tooth. Pleura of first four segments with a ventrally directed acute tooth on distal margin (character apparent only in large adults). Fifth and sixth segments with tooth at posterolateral corner of pleura, that of fifth often small and rectangular. Abdominal grooves deep and well defined. First segment with posteromedian and anteromedian grooves connected ventrally. Second segment with anterior and posterior tergal grooves connected dorsally; anterior and median pleural grooves connected dorsally and ventrally; a thin and more or less interrupted posterior pleural groove connected with posterior tergal. Telson usually lacking subterminal spines.

Measurements.—Length of body: 74 mm.

Variations.—Position of the posterior rostral tooth is variable. In some individuals this tooth



FIGURE 27.—*Sicyonia typica* (Boeck). Carapace and first abdominal segment in lateral view, 1 mm. indicated (after Lunz, 1945).

is located behind the orbital margin, thus appearing as one of the carinal series on the carapace (Lunz, 1945).

Color.—Blue spots in tail prominent in life; bright red blotch surrounding rostrum (note by W. L. Schmitt in U.S. National Museum records).

Habitat.—Between tide marks to 37 fathoms.

Type locality.—Molde Fjord, west coast of Norway [erroneous locality, evidently incorrectly labeled].

Known range.—Beaufort, N.C.; east and west Florida; Gulf of Campeche; Cuba through West Indies to Rio de Janeiro, Brazil.

Remarks.—Hildebrand (1954) stated that this species is taken in commercial quantities in the Gulf of Batabano off southwest Cuba, and occurs in commercial but unexploited quantities in parts of the Gulf of Campeche.

There remains some doubt that this species occurs in North Carolina, though Lunz (1945) stated that it does. If so, it is not common.

Sicyonia dorsalis Kingsley

Figure 28

Sicyonia dorsalis Kingsley, 1878b, p. 97.—Hay and Shore, 1918, p. 380, pl. 25, fig. 3.

Eusicyonia dorsalis: Burkenroad, 1934b, p. 121, figs. 13, 14 (rev.).—Lunz, 1945, p. 8, fig. 5.

Recognition characters.—Body small, slightly compressed. Carapace minutely punctate, less deep and inflated than *S. stimpsoni*. Rostrum extending horizontally or decurved variable distance beyond eye; ridge on lateral surface sloping upward to near dorsal margin; armed dorsally with three teeth not counting tip, posterior tooth in front of orbital margin and placed variable distance from anterior carinal tooth of carapace; tip appearing bifurcate, dorsal tooth greatly enlarged, ventral tooth reduced to blunt angle.



FIGURE 28.—*Sicyonia dorsalis* Kingsley. Carapace and first abdominal segment in lateral view, 2 mm. indicated (after Lunz, 1945).

Postrostral carina with two teeth, anterior tooth before level of hepatic spine, posterior tooth near midpoint. Antennal angle armed with a spine.

Abdominal segments with conspicuous tergal carinae; margins of notches at posterior ends of carinae on segments three to five sometimes produced into long slender spines. First abdominal segment with tergal carina produced into an elevated anterior tooth; anteroventral margin of pleura concave (or at least straight in young) and with an anterior angle in addition to one in middle of ventral edge, posterior angle sometimes produced into a dentiform projection. Second abdominal segment with tergal and pleural grooves connected as an uninterrupted groove extending full depth of segment. Ventral margins of pleura in segments three and four each with both anterior and posterior angle, anterior sometimes sharp, posterior sometimes armed with strong curved spine. Fifth segment with posterior spine only. Tergal carina of sixth segment extended into a posterior spine.

Petasma of male with distoventral lobe forked.

Measurements.—Length of body: male 63 mm.; female 71 mm.

Variations.—Angles and spines on the pleura become better defined with increasing age.

Habitat.—Common on mud bottom (Hildebrand, 1954), or mud and shells (Holthuis, 1959); from 3 to 88 fathoms, rarely to 230 fathoms.

Type locality.—Fort Jefferson, Dry Tortugas, Fla.

Known range.—Cape Hatteras, N.C., to Texas; Colombia to French Guiana.

Remarks.—Hildebrand (1954, 1955) listed this species as third in abundance on the brown shrimp grounds in Texas but less common on Campeche Banks. It is most common in 15–25 fathoms but ranges shoreward to depths of 6.5 fathoms, and small specimens were occasionally taken in the mouths of bays. Eldred (1959) listed this species as the most common among *Sicyonia* species taken in the Tortugas controlled area in Florida.

Adults of this species fouled with the barnacle, *Balanus amphitrite niveus* Darwin, and *Polydora* sp., were reported from the Gulf of Mexico off Marquesas Key by Eldred (1962). Such specimens, ranging in size from 58 to 70 mm. total length, were judged to be near maximum size for the species.

Figure 29

Sicyonia stimpsoni Bouvier, 1905, p. 748.—Holthuis, 1959, p. 75.

Sicyonia dorsalis: Milne Edwards and Bouvier, 1909, p. 253, text-figs. 86-88, pl. 8, figs. 4-13.

Eusicyonia stimpsoni: Burkenroad, 1934b, p. 121 (notes).—1939, p. 57.

Eusicyonia edwardsei: Schmitt, 1935a, p. 133, fig. 6.

Recognition characters.—Rostrum usually elevated at considerable angle, extending variable distance beyond eye; with three dorsal teeth not counting tip, posterior tooth in front of orbital margin separated by a variable distance from anterior carinal tooth of carapace; tip often appearing bifurcate but a third ventral tooth present behind or below level of anterior cleft; a slight ridge on lateral surface running parallel with ventral margin. Postrostral carina with two teeth, anterior tooth before level of hepatic spine, posterior tooth behind midpoint; sometimes rudiment of a third tooth appearing as a minute crest-like swelling with truncated anterior edge a little in front of posterior tooth. Antennal angle armed with a spine.

Abdominal segments with conspicuous tergal carinae. First segment with carina produced into an elevated anterior tooth. Margins of dorsal notches at posterior ends of segments three to five produced as short angular projections. A tooth at posterior end of fourth to sixth segments. Segments one to four with a ventral spine on pleura; segments five and six with spine at posteroventral corner. Second abdominal segment with pleural groove curving forward midlaterally, not connected to short tergal groove curving downward and backward.



FIGURE 29.—*Sicyonia stimpsoni* Bouvier. Carapace and portion of first abdominal segment in lateral view, 2 mm. indicated (after Lunz, 1945).

Petasma of male with distoventral lobe not forked.

Measurements.—Length of body: male, 44 mm.; female, 60 mm.

Variations.—Pleural spines may be absent in young individuals.

Color.—Branchial region of carapace with orange, or brownish and yellowish-white ring in posterior half (Holthuis, 1959). North Carolina specimens show a purple spot with surrounding vermilion ring in this region.

Habitat.—Found on predominantly mud and shell bottom in Surinam (Holthuis, 1959); shallow water to 230 fathoms.

Type locality.—Off Barbados, British West Indies, lat. 13°03'05" N. long. 59°36'18" W., depth 103 fathoms.

Known range.—Cape Hatteras, N.C., to Campeche Gulf; West Indies to French Guiana.

Remarks.—Among species of *Sicyonia* occurring in the Carolinas, the only detailed description of development is that given by Pearson (1939) for this species. Eggs attributed to this species were taken in inlets, and larval development (reconstructed from plankton) proceeded through five naupliar, three protozoal, and two mysis stages. Eggs were taken abundantly at St. Augustine Inlet, Fla., in plankton, from March 30 to August 8; they were taken in lesser abundance from January to March, and August to September at Fort Pierce, Fla., and off Stono Inlet, S.C., in September. Naupliar and protozoal stages were found from April to August, and mysis stages were found in January and August-September. Thus, the breeding season along that stretch of coast lasts at least from January to September.

Holthuis (1959) noted that males in Surinam material outnumbered females about 3 to 1.

Family Sergestidae

Penaeidea with last two pairs of legs reduced in size or lost; gills few or lost.

KEY TO SUBFAMILIES AND SPECIES IN THE CAROLINAS

a. Head not greatly elongated; gills present

Sergestinae; *Acetes americanus caroliniae* (p. 39).

aa. Head greatly elongated; gills absent

Luciferinae; *Lucifer faxoni* (p. 40).

Subfamily Sergestinae

Carapace moderately compressed. Inferior antennular flagella present; with prehensile organ in male. Second and third pair of legs, at least, terminated by a pincer. Gills present. Sixth abdominal segment and telson without sexual differences; without protuberances or ventral processes in males. Petasma with a short base. No protuberance on peduncle of first pleopod (after Hansen, 1922).

Genus *Acetes* Milne Edwards, 1830

Burkenroad, 1934a, p. 99.—1934b, p. 126.

Acetes americanus carolinae Hansen

Figures 30–31

Acetes americanus Ortmann, 1893, p. 39, pl. 2, fig. 2.

Acetes carolinae Hansen, 1933, p. 31, figs. 1–8.

Acetes americanus carolinae: Holthuis, 1959, p. 49, fig. 1, a–c (rev.).

Recognition characters.—Body small. Integument thin, smooth, polished. Carapace with rostrum elevated, short; a single tooth behind acute tip. A prominent spine on rounded ridge behind eye; hepatic spine small. Eyes prominent, stalk conical, cornea large. Antennules with peduncle long, third article more than twice length of second article, lower flagellum much shorter and more slender than upper, upper hairy ventrally near base; in males, curved lower flagellum forming clasping organ, basal four annulations thicker than distal annuli, third and fourth armed dorsally with a short row of spines, distal one strongest. Antennal scale reaching end of second article of antennular peduncle in males, beyond end of second article in females.

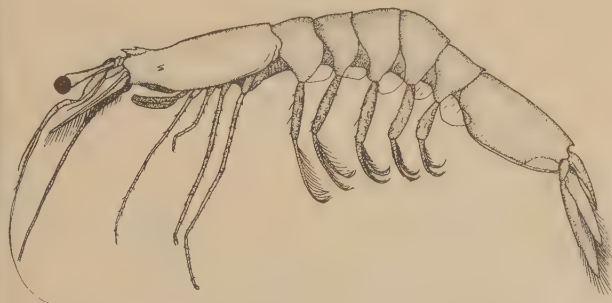


FIGURE 30.—*Acetes americanus carolinae* Hansen. Female in lateral view, $\times 4.8$.

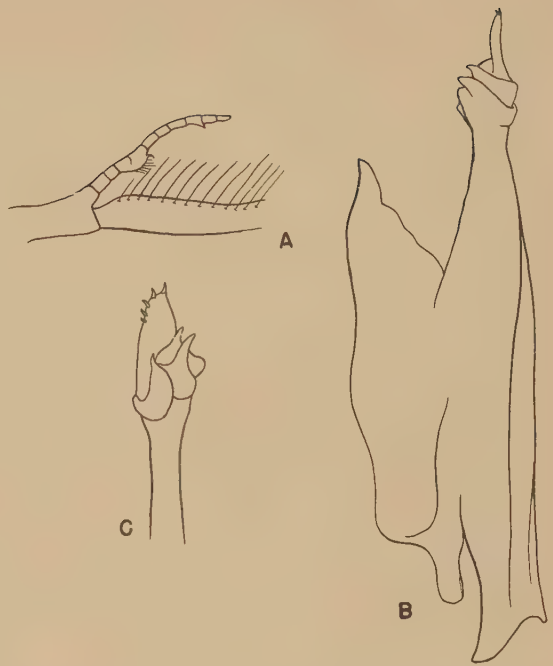


FIGURE 31.—*Acetes americanus carolinae* Hansen.

A, clasping organ on antennule of male $\times 50$; B, petasma of male, right side in posterior view $\times 90$; C, tip of petasma, anterior view of right side $\times 90$.

Sixth segment of abdomen with convex ventral margin bifurcated caudally. Exopod of uropod about 4.5 times longer than broad; proximal three-fifths of outer margin smooth, ending in a minute tooth, remainder of margin hairy.

Petasma of male with membranous, triangular-tipped external portion exceeded by slender median part; median portion ending in complicated capitulum, a distomedian crooked lobe tipped with four thick, short spines, and three other shorter lateral lobes each produced into an acute point. Lobes behind base of last pair of legs greatly enlarged in males forming genital coxae broader than long. Coxae of third legs in females with posteromedian corner produced into a protuberance; sternite immediately behind third legs bearing two curved projections forming a U-shaped thelycum.

Measurements.—Length of body: 15 to 26 mm.

Variations.—Holthuis (1948, 1959) followed Burkenroad (1934a) in considering the known species of *Acetes* from the western Atlantic with one tooth behind the tip of the rostrum to be all

A. americanus. Burkenroad recognized four subspecies: *A. americanus americanus* Ortmann, Brazil; *A. a. limonensis* Burkenroad, Panama; *A. a. louisianensis* Burkenroad, Louisiana; *A. a. carolinae* Hansen, North Carolina. Holthuis considered these to be clinal variants, with the northern and southern representatives differing most widely from each other. Females of the four doubtfully valid subspecies differ in depth of the concavity in the middle of the posterior segment of the genital sternite. This structure is deeper than broad in Carolinian specimens, but becomes shallower in progressively more southern forms. Holthuis suggested that the extreme northern and southern forms might deserve to retain subspecific rank.

Color.—Nearly transparent with faint red flecks.

Habitat.—Littoral oceanic and estuarine waters to 23 fathoms.

Type locality.—Typical form, mouth of Pará (=Tocantins) River, [State of Pará], Brazil. Northern form, off Beaufort Inlet, N.C.

Known range.—Cape Lookout, N.C., to mouth of Pará River, Brazil.

Remarks.—Burkenroad (1934b) found larval stages of this *Acetes* at the surface of the outer littoral of Louisiana in spring. He described the spermatophore as gourd-shaped, much as the spermatophore of *Lucifer*, and gave other structural details of the reproductive system.

In Bogue Sound, near Beaufort Inlet, N.C., specimens have been taken in every month of the year in a large plankton net fished from a pier at the surface on flood tides at night. Gutsell (in Hansen, 1933) reported that this species can sometimes be taken near Beaufort Inlet, N.C., "in gallons at a time," especially in late summer and early fall.

Subfamily Luciferinae

Carapace extremely compressed. Antennules without inferior flagella in both sexes. Third pair of legs only terminated by a pincer. Gills absent. Sixth abdominal segment of male with two ventral processes, second far behind first. Telson of male with a strong protuberance on internal face. Petasma sessile, proximal part fixed like a large disc on peduncle of first pleopod; each peduncle,

near disc, possessing a protuberance with distal spines (after Hansen, 1922; Burkenroad, 1934b).

Genus *Lucifer* Thompson, 1829

Hansen, 1919, p. 48.

Lucifer faxoni Borradaile

Figure 32

Lucifer faxoni Borradaile, 1915, p. 227.—Hay and Shore, 1918, p. 381, text-fig. 4, pl. 26, fig. 10.—Holthuis, 1959, p. 52 (rev.).

Recognition characters.—Body small, thin; integument smooth, thin, transparent. Anterior portion of cephalothorax cylindrical, greatly lengthened (about 1.5–2.5 times longer than posterior portion), bearing eyes, antennules, and antennae far in front of mouth parts and legs. Rostrum small, a spine on each side behind eye and at anterolateral corner. Posterior portion of cephalothorax with spine on each side in front. Eyes large, prominent, on stout conical stalks about one-fourth to one-third length of anterior part of cephalothorax. Peduncles and flagella of antennules long, slender. Peduncle of antennae about half as long as first article of antennular peduncle; flagellum longer than that of antennule; antennal scale almost linear, fringed on inner margin with long hairs.

Third maxilliped long, pediform. Three pairs of legs; first pair short; last two pairs of equal length extending almost to end of cephalothorax.

Abdomen much compressed; segments deepest and produced into spiniform angle where pleopods originate. Sixth segment as long as preceding two segments, posterolateral angles spiniform near

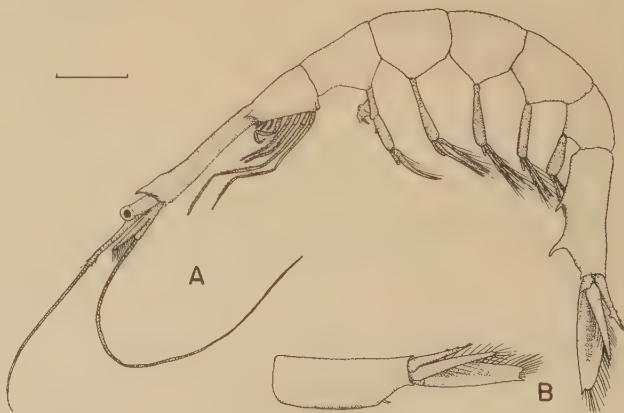


FIGURE 32.—*Lucifer faxoni* Borradaile. A, male in lateral view; B, sixth abdominal segment and tail fan of female in lateral view; 1 mm. indicated.

base of uropods; a small median spine above base of telson; male with two strong ventral spines, posterior spine curved and about twice length of anterior spine. Telson slender, about half length of uropods; truncate distally with a strong spine at each corner; two pairs of intermediate spines on distal border, and two pairs of lateral spines about equidistant; males with a prominent ventral projection on distal half. Outer ramus of uropod longer and broader than inner.

Petasma of male membranous, folded, foliaceous; ventral process needlelike, curved, tapering to acute end directed ventrolaterally.

Measurements.—Length of body: 10–12 mm.

Color.—Almost perfectly transparent in life.

Habitat.—Oceanic and estuarine waters from surface to 50 fathoms.

Type locality.—Off Chesapeake Bay.

Known range.—Off Nova Scotia along coast of United States to Louisiana; through West Indies and along coast of South America to off Rio de Janeiro, Brazil; Bermuda and mid-Atlantic (lat. 42°50'26" N. long. 41°48' W., lat. 41°39'34" N. long. 39°21' W., and lat. 4°30' N. long. 28°20' W.); Rea Sea; Malay Archipelago; Marshall Islands; Hawaiian Islands; Fanning Island (Holthuis, 1959).

Remarks.—This interesting little shrimp is abundant near Beaufort Inlet, N.C., throughout most of the year (collected from February through October), and often occurs in swarms outside the harbor.

Brooks (1882) worked out the larval development of a species of *Lucifer* in the Beaufort, N.C., area, and from his figures and present knowledge of distribution, it is almost certain that he was dealing with *L. faxoni*. Brooks found egg-bearing females only in April, but found larvae as late as September. Since then, egg-bearing females have been found through the summer into October in Bogue Sound near Morehead City, N.C. Brooks illustrated the egg, a number of larval stages (two nauplius, three protozoa, one zoea, one schizopod, one mastigopus, and one lucifer), and a final adult stage in males.

As various authors have pointed out, Brooks mistakenly thought that the species was primarily estuarine, the adults leaving the marshes on ebb tides to spawn in the ocean, because he found the species most concentrated in the estuary near

Beaufort on ebb tides. He failed to find specimens on flood tide. The species can be found in estuaries on both flood and ebb tide, but its primary home is the ocean.

Burkenroad (1934b) reported a female with large ova from the outer littoral of Louisiana. He gave a detailed account of the reproductive systems of males and females showing that they are fully bilateral and not asymmetrical as stated by Brooks (1882), Bate (1888), and Hansen (1922). The males, however, carry but one spermatophore at a time, possibly because the body is so strongly compressed.

Section Caridea

Pleura of second abdominal segment overlapping those of first and third segments. Third legs never with chelae. Gills phyllobranchiate (Holthuis, 1955).

Family Pasiphaeidae

Rostrum small or obsolete. Mandibular palp absent, one or two jointed. Legs with exopods; first two pairs of legs chelate, chelae slender, cutting edges pectinate; third, fourth, and fifth legs smaller than chelipeds, fourth generally smallest (Rathbun, 1901; Holthuis, 1955).

Genus *Leptochela* Stimpson, 1860

Stimpson, 1860, p. 111.—Hemming, 1958b, p. 157.

Leptochela serratorbita Bate

Figures 33–34

Leptochela serratorbita Bate, 1888, p. 859, pl. 139, fig. 1.—Rathbun, 1901, p. 127.—Schmitt, 1935a, p. 134.

Recognition characters.—Carapace smooth, anterior half with low carina. Rostrum nearly horizontal, unarmed, about as long as eyestalks. Upper portion of orbits finely serrated or spinulose.

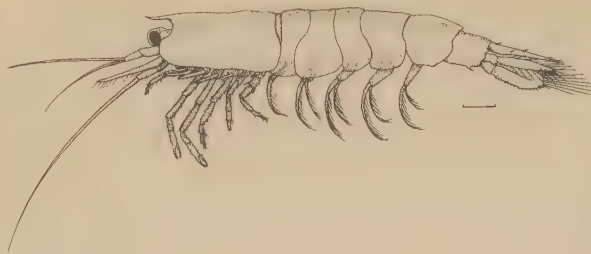


FIGURE 33.—*Leptochela serratorbita* Bate. Animal in lateral view, 1 mm. indicated.

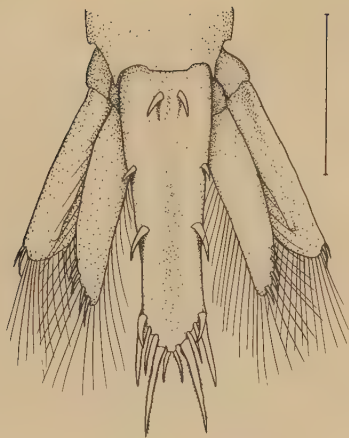


FIGURE 34.—*Leptochela serrator-bita* Bate. Uropods and telson in dorsal view, 1 mm. indicated.

Antennal spine small or absent. Antennular peduncle reaching beyond middle of antennal scale.

First two pairs of legs chelate; fingers a little longer than palm, cutting edges pectinate.

Abdomen with fourth and fifth segments broadly carinate; sixth segment with an anterior middorsal tubercle, a posterior spine either side of middle and a prominent spine preceding each posterolateral angle. Telson with an anterior submedian pair of spines and three pairs of lateral marginal spines, anterior lateral spines at anterior fourth, second at middle, third near posterior extremity; tip with three pairs of unequal spines and two pairs of strong setae, all more or less fimbriated. Exopod of uropod with a row of spines along ventrolateral border, a long curved spine at tip; endopods spiny near tip.

Measurements.—Length of body: 21 mm.

Habitat.—Known only from coastal and occasionally estuarine waters, from surface to 23 fathoms (perhaps to 33 fathoms).

Type locality.—St. Thomas, shallow water.

Known range.—Near Beaufort Inlet, N.C.; Charleston Harbor, S.C.; Key West, Fla.; Puerto Rico, and Virgin Islands.

Remarks.—This small shrimp has been taken in May, July, October, and November in surface plankton tows in Bogue Sound, near Beaufort Inlet, N.C., on flood tides at night. The specimen taken in May was ovigerous. Lunz (1939) collected a specimen in July in South Carolina.

Family Palaemonidae

Caridea having first two pairs of legs chelate, second pair usually larger than first, carpus of second pair not subdivided. Rostrum usually armed with teeth and not movable. Mandibles usually with an incisor process (Holthuis, 1951a).

KEY TO SUBFAMILIES IN THE CAROLINAS

- a. Posterior margin of telson with three pairs of spines
Pontoniinae (p. 42).
- aa. Posterior margin of telson with two pairs of spines
and two or more setae.....Palaemoninae (p. 50).

Subfamily Pontoniinae

Upper antennular flagellum with both rami fused in basal part. Appendix masculina generally present on second pleopod of male; appendix interna on second pleopod of female. Pleurobranch absent from third maxilliped. Posterior margin of telson with three pairs of spines (Holthuis, 1951a).

KEY TO GENERA AND SPECIES IN THE CAROLINAS

(Holthuis, 1951a, modified)

- a. All maxillipeds with well-developed exopods.
 - b. Hepatic spine present.....*Periclimenes* (p. 42).
 - c. Antennal spine absent; dactyls of last three legs bifurcate.....*P. longicaudatus* (p. 42).
 - cc. Antennal spine present; dactyls of last three legs simple.....*P. americanus* (p. 43).
- bb. Hepatic spine absent.
 - c. Rostrum compressed, with distinct teeth
Periclimenaeus (p. 45).
 - d. Antennal scale with no terminal tooth
P. schmitti (p. 45).
 - dd. Antennal scale with terminal tooth
P. wilsoni (p. 46).
 - cc. Rostrum depressed, with at most two small teeth near tip.....*Pontonia* (p. 47).
 - d. Dorsal spines of telson small and rather inconspicuous.....*P. domestica* (p. 47).
 - dd. Dorsal spines of telson well developed
P. margarita (p. 48).
- aa. Second and third maxillipeds without exopods
Neopontonides beaufortensis (p. 49).

Genus *Periclimenes* Costa, 1844

Subgenus *Periclimenes* Costa, 1844

Holthuis, 1951a, p. 23, 26.—Hemming, 1958b, p. 159.

Periclimenes (*Periclimenes*) *longicaudatus* (Stimpson)

Figure 35

Urocaris longicaudata Stimpson, 1860, p. 39.—Hay and Shore, 1918, p. 394, pl. 27, fig. 7.

Periclimenes (*Periclimenes*) *longicaudatus*: Holthuis, 1951a, p. 26, pl. 6, figs. a-m; pl. 8, fig. m (rev.).

Recognition characters.—Rostrum straight, short, reaching to end of second or third article

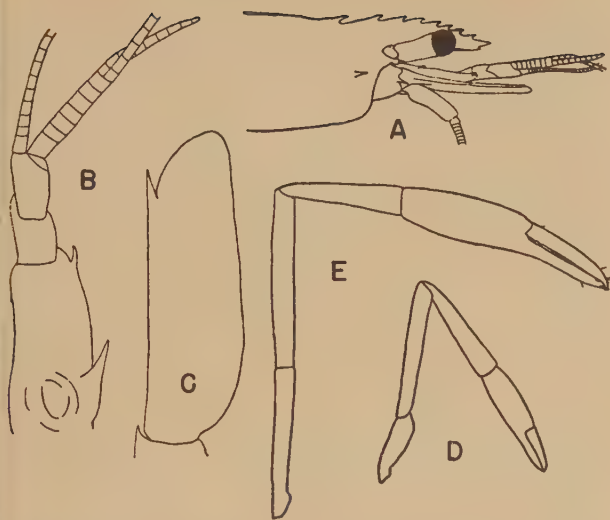


FIGURE 35.—*Periclimenes* (*Periclimenes*) *longicaudatus* (Stimpson). A, anterior part of body in lateral view, $\times 5$; B, antennule, $\times 11.5$; C, antennal scale, $\times 11.5$; D, first leg, $\times 13.0$; E, second leg, $\times 13.0$ (after Holthuis, 1951a).

of antennular peduncle; upper margin raised into a high arcuate crest with seven to nine teeth, first two teeth behind orbit more widely spaced than distal teeth; lower margin with one or two small spines near tip. Carapace with lower angle of orbit produced into a lobe constricted at base; supraorbital and antennal spines absent; anterolateral angle rounded. Eyes well developed and elongate. Stylocerite well developed but not reaching to middle of basal antennular article; basal antennular article convex and ending in a strong spine; upper antennular flagellum with two rami fused for four to eight joints. Antennal scale with outer margin slightly concave, ending in a strong tooth exceeded distally by lamella; antennal peduncle reaching almost to middle of scale, with distinct outer spine near base of scale. All maxillipeds with well-developed exopods.

First legs slender, reaching almost to end of antennal scale; second legs equal in size and shape, stronger and longer than first legs.

Abdomen smooth; all pleura rounded. Third abdominal segment somewhat produced in middle of posterior margin. Sixth abdominal segment twice length of fifth and longer than telson. Telson with two pairs of dorsal spines both lying behind middle; posterior margin with three pairs of spinules.

Measurements.—Length of body: male, 17 mm.; ovigerous females, 15 to 22 mm.

Color.—Body transparent in life.

Habitat.—This species is found in abundance on submerged vegetation along with *Hippolyte* and *Tozeuma*, on *Leptogorgia*, algae and *Sargassum*, or from sponges (Schmitt, 1924b); however, it is hard to detect because of its almost perfect transparency. Surface to 6 fathoms, rarely to 15 fathoms.

Type locality.—Coast of Carolina.

Known range.—Hatteras, N.C., to southwestern Florida; West Indies to State of Paraíba, Brazil. There are doubtful records from the Indian Ocean and deeper waters of the Gulf of Mexico (Holthuis, 1951a).

Remarks.—This species is abundant in the Beaufort, N.C., area, and has been collected there throughout the year. Ovigerous females have been found from May through October. They occur in Cuba in January and March (Schmitt, 1924b) and in Texas in May. Pearse and Williams (1951) found the form on reefs off the North Carolina coast along with an unidentified *Periclimenes*. Last larval, postlarval, and early juvenile stages doubtfully assigned to this species have been described by Gurney and Lebour (1941) from Bermuda.

Subgenus *Harpilius* Dana, 1852

Holthuis, 1951a, p. 23.

Periclimenes (*Harpilius*) *americanus* (Kingsley)

Figure 36

Anchistia americana Kingsley, 1878b, p. 96.

Periclimenes (*Harpilius*) *americanus*: Holthuis, 1951a, p. 60, pl. 18, figs. a–j; pl. 19, figs. a–e (rev.).

Recognition characters.—Rostrum rather high and straight; tip directed upward, reaching about to end of antennular peduncle; upper margin nearly straight, with 7–10 teeth, first two behind orbit and considerably separated; lower margin with 2, sometimes 3 teeth but with an unarmed stretch before tip. Carapace with only antennal and hepatic spines; lower orbital angle acute; postorbital ridge paralleling orbit; anterolateral angle broadly rounded. Eyes well developed; cornea globular, two dark-colored bands visible on cornea in fresh material; an ocellus present. Stylocerite rather strong, sharply pointed, almost reaching middle of basal antennular article; outer

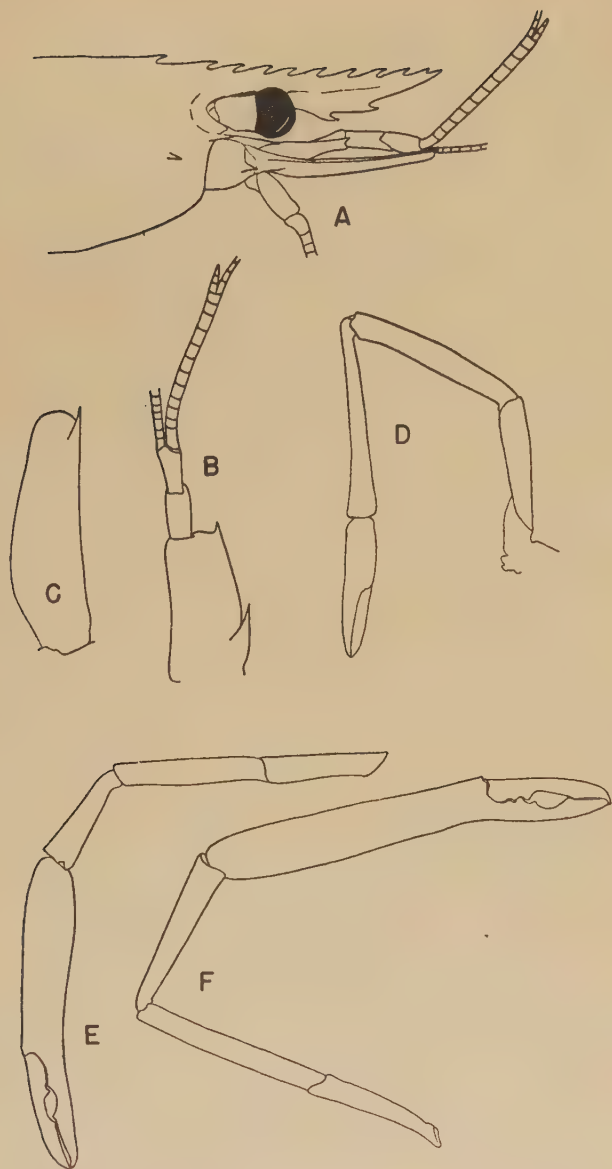


FIGURE 36.—*Periclimenes (Harpilius) americanus* (Kingsley). A, anterior part of body in lateral view, $\times 8.5$; B, antennule, $\times 11$; C, antennal scale, $\times 11$; D, first leg, $\times 11$; E, F, second leg (different specimens), $\times 7.5$ (after Holthuis, 1951a).

margin of basal antennular article convex, ending in well-developed anterolateral tooth; second and third articles elongate, second slightly shorter than third; upper antennular flagellum with 2 rami fused for 8–12 joints (often 6 in younger specimens), free portion of shorter ramus with 3 or 4 joints, length less than one-fourth that of fused part. Antennal scale slightly exceeding

antennular peduncle, outer margin straight or slightly concave and ending in a strong tooth slightly exceeding distally narrowed lamella; scale with a distinct spine near base; antennal peduncle not reaching to middle of scale. All maxillipeds with well-developed exopods.

First legs slender; chela and sometimes a small portion of carpus extending beyond antennal scale; fingers smooth, as long as palm. Second legs equal in size and shape, very strong and longer than first; adult males with fingers less than half as long as palm, three or four teeth on cutting edges leaving gape at midlength when closed; second legs shorter and fingers not agape in juveniles and adult females.

Abdomen with pleura of first four segments rounded, of fifth ending in a small tooth; median posterior margin of third only slightly produced posteriorly. Sixth segment about 1.5 times as long as fifth and about three-fourths length of telson. Telson with two dorsal pairs of spines at one-third and two-thirds length; posterior margin with three pairs of spines, intermediate pair less than twice length of inner spines.

Measurements.—Length of body: male 22 mm.; ovigerous females, 13 to 20 mm.

Variations.—The carpus of the second pair of legs varies in length as do the dactyls of the last three pairs of legs.

Color.—Ground color translucent grayish white; carapace with three oblique orange-brown lateral lines and a pair of dorsal lines running back from base of rostrum; each abdominal segment crossed by a narrow brown band and a row of small dark spots on posterior margin; tail fan with two larger lateral and median spots and an orange-brown tip (Verrill, 1922).

Habitat.—This species lives in coastal waters, preferring sandy or rocky bottom, often between algae or coral. Verrill (1922) found large schools near the surface in Bermuda, and Gurney (1943a) found it to swim singly or in small numbers at the surface at night in certain periods of the lunar cycle (see Holthuis, 1951a). Shallow water to 40 fathoms.

Type locality.—Key West, Fla.

Known range.—Beaufort, N.C.; Jupiter Inlet, Fla., to west coast of Florida off Hernando County; off Cape Catoche, Yucatan, Mexico; through West Indies to Aruba; Bermuda.

Remarks.—Gurney (1943a) listed this species as one of the commonest decapod crustaceans in the littoral region of Bermuda. Females outnumbered males two to one; however, ovigerous females were never collected there. From plankton, Gurney (1936c, 1943a) described the first and fifth larval, and the first postlarval stages, and gave remarks on allometric growth of the second legs. These legs are stronger and longer in males than in females, with fingers agape in old males. The center of greatest growth is in the palm.

Ovigerous females have been found from January to May and from September to November in Florida, the West Indies, and South America.

Holthuis (1951a) listed *P. americanus* as common in North Carolina, but it has been taken only once (August 5, 1958) in surface plankton tows in Bogue Sound that have produced hundreds of *P. longicaudatus*.

Genus *Periclimenaeus* Borradaile, 1915

Holthuis, 1951a, p. 76.—Hemming, 1958b, p. 159.

Periclimenaeus schmitti Holthuis

Figure 37

Periclimenaeus schmitti Holthuis, 1951a, p. 90, pl. 27, figs. a-m.

Recognition characters.—Rostrum short, straight, or somewhat decurved, not reaching to end of basal article of antennular peduncle; upper margin bearing one or two teeth, exclusive of upturned tip; lower margin convex, unarmed. Carapace smooth; postorbital ridge paralleling orbit, extending from strong antennal spine dorsally and becoming gradually obsolete; anterolateral angle broadly rounded, produced forward. Eyes well developed, cornea globular, shorter and narrower than eyestalk. Basal article of antennular peduncle with short, broad, blunt tipped stylocerite reaching about to middle of article; outer margin with blunt angle at level of stylocerite tip, concave beyond angle, anterolateral angle of article with rather large tooth; second and third articles short; upper antennular flagellum with three fused joints, free part of short ramus with one short joint. Antennal scale broadly ovate; outer margin nearly straight, with no terminal tooth.

First leg with carpus and chela extending beyond antennal scale; chela slender, fingers two-thirds length of palm, unarmed, carpus about as

long as chela, slightly shorter than merus. Second legs unequal, both reaching with chela and part of carpus beyond antennal scale. Larger second leg heavy, fingers slightly less than half as long as palm, inwardly curved; upper margin of dactyl broadly rounded, cutting edge finely denticulate distally, with large rectangular-shaped tooth fitting into pit on immovable finger when closed; fixed finger with strong, narrow tooth at inner margin of pit; palm swollen, covered with a number of small scalelike tubercles; carpus conical, about one-fourth length of palm; merus about one-third length of palm, sometimes with small tubercles at lower edge. Smaller second leg with fingers straight, slightly shorter than one-third length of palm; cutting edge of dactyl denticulate throughout, that of fixed finger straight; tubercles on palm fewer than on opposite member. Third leg with propodus and part of

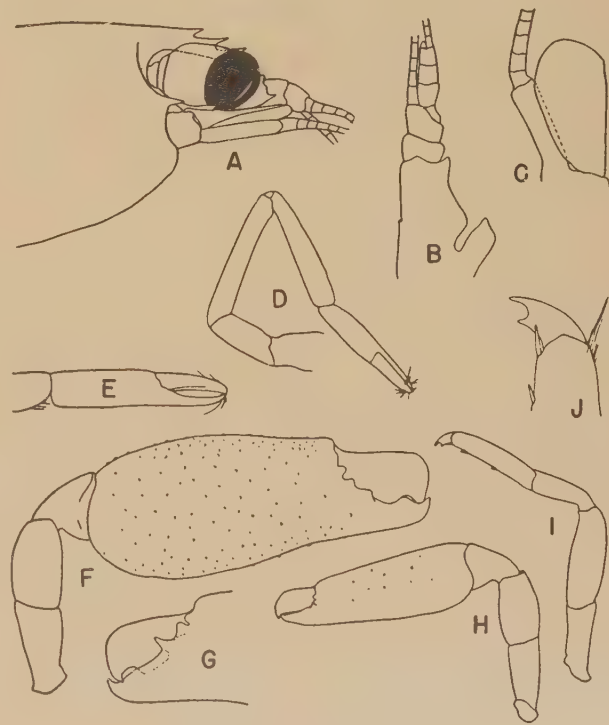


FIGURE 37.—*Periclimenaeus schmitti* Holthuis. A, anterior part of body in lateral view, $\times 17$; B, antennule, $\times 22.5$; C, antenna, $\times 22.5$; D, first leg, $\times 22.5$; E, chela of first leg, $\times 33.5$; F, larger second leg, outside, $\times 15$; G, fingers of larger second leg, inside, $\times 15$; H, smaller second leg, $\times 15$; I, third leg, $\times 15$; J, dactyl of third leg, $\times 56.5$ (after Holthuis, 1951a).

carpus reaching beyond antennal scale, dactyl short, distinctly bifurcate.

Abdomen smooth; pleura of first five segments rounded; sixth segment about as long as fifth and about two-thirds length of telson. Telson with two pairs of small dorsal spines somewhat removed from lateral margin, placed at one-third and two-thirds length; six spines on posterior margin placed in one row, intermediate spines longest. Uropods broadly ovate, exopod with outer margin ending in a tooth flanked medially by a movable spine.

Measurements.—Length of body: ovigerous female, 20 mm.

Variations.—Specimens with a single rostral tooth are young.

Habitat.—Shallow water.

Type locality.—Tortugas, Fla.

Known range.—Bogue Sound, N.C.; Tortugas, Fla.

Remarks.—Two specimens from North Carolina were taken August 16, 1957, in a nighttime surface plankton tow on flood tide near Beaufort Inlet. Though these have intermediate spines on the telson longer than the other terminal pairs, they agree well with specimens of *P. schmitti* from Tortugas.

***Periclimenaeus wilsoni* (Hay)**

Figure 38

Coralliocaris wilsoni Hay, 1917, p. 71.—Hay and Shore, 1918, p. 394, text-fig. 13; pl. 27, fig. 8.

Periclimenaeus wilsoni: Holthuis, 1951a, p. 103, pl. 31, figs. a-m; pl. 32, figs. b-c (rev.).

Recognition characters.—Rostrum nearly straight or somewhat decurved, almost reaching end of antennular peduncle; upper margin somewhat convex, bearing 10 to 12 regularly spaced teeth, first tooth directly over or immediately behind orbital margin; lower margin straight or concave, unarmed. Carapace smooth with only an antennal spine placed close to acute lower orbital angle; postorbital ridge paralleling orbit indistinct; anterolateral angle somewhat anteriorly produced, broadly rounded. Eyes well developed. Stylocerite of antennular peduncle broad, short, and pointed, almost reaching middle of basal article; outer margin of basal article with a blunt angle near tip of stylocerite, concave beyond angle, ending in a strong tooth; second

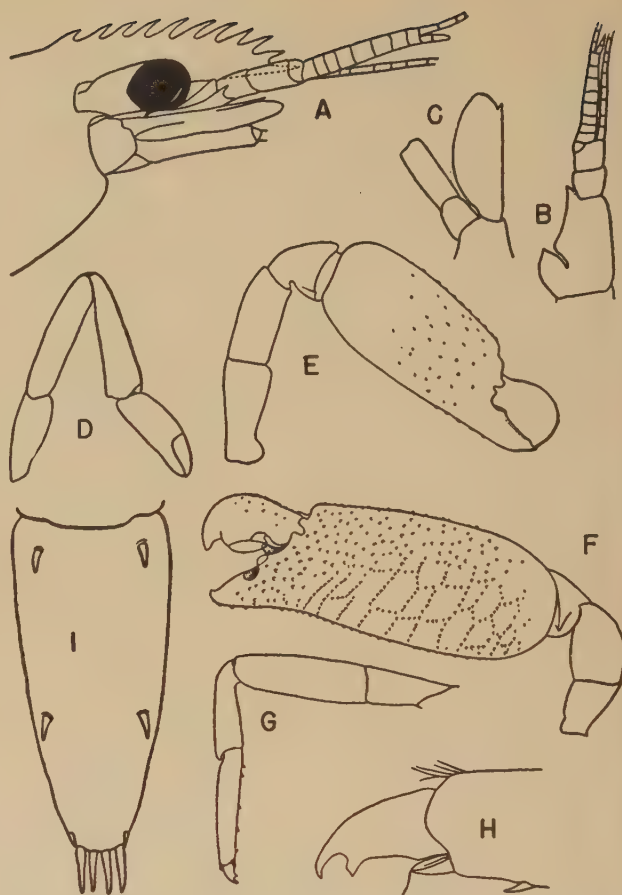


FIGURE 38.—*Periclimenaeus wilsoni* (Hay). A, anterior part of body in lateral view, $\times 11.5$; B, antennule, $\times 9.5$; C, antenna, $\times 9.5$; D, first leg, $\times 9.5$; E, smaller second leg, $\times 9.5$; F, larger second leg, $\times 4.5$; G, third leg, $\times 9.5$; H, dactyl of third leg, $\times 56$; I, telson in dorsal view, $\times 17$ (after Holthuis, 1951a).

and third antennular articles about same size; upper antennular flagellum with six to nine fused joints; free part of short ramus with two joints. Antennal scale a little longer than antennal peduncle; outer margin straight, ending in a small spine; lamella broadest proximally.

First legs with carpus and chela extending beyond tip of antennal scale; chela rather thickset; fingers shorter than palm, unarmed; carpus about as long as merus. Second legs strong, unequal, with part of carpus and chela extending beyond tip of antennal scale. Larger second legs with chela almost equal to bulk of body; fingers inwardly curved, somewhat less than half length of palm; dactyl with upper margin convex, cut-

ting edge with large rectangular tooth fitting into pit on immovable finger when closed; immovable finger with distinct tooth at inner margin of pit; palm swollen, tuberculate at base and on base of fingers, tubercles on proximal lower part of palm arranged in rows or honeycomb pattern; carpus smooth, short, cup-shaped; merus about one-third length of palm. Smaller second leg much as larger one in general shape; palm somewhat swollen, with scattered tubercles anteriorly. Third leg with greater part of propodus reaching beyond tip of antennal scale; dactyl short, broad, bifurcate.

Abdomen smooth; pleura of first five segments broadly rounded; sixth segment half length of telson. Telson with two pairs of dorsal spines somewhat removed from lateral margin, anterior pair close to anterior margin, posterior pair slightly behind midlength; posterior margin with three pairs of spines, outer pair short and located in advance of larger intermediate and inner pairs. Uropods broadly ovate, outer margin of exopod ending in a tooth flanked medially by a movable spine.

Measurements.—Length of body: male, 20 mm.; ovigerous females, 16 to 20 mm.

Variations.—Juveniles may have a shorter rostrum with fewer dorsal teeth, and in some specimens the second chelae may be smooth.

Color.—Clear, milky white; integument so transparent that color of internal organs is plainly visible; egg masses light bluish green.

Habitat.—This species is known to live in sponges in coastal waters in company with *Synalpheus longicarpus* and *S. townsendi*; 10–40 fathoms.

Type locality.—Fishing grounds, 20 miles off Beaufort Inlet, N.C.

Known range.—Off Beaufort, N.C.; off Loggerhead Key, near Tortugas, and Franklin County, Fla.

Remarks.—Ovigerous females have been reported from Florida in July and North Carolina in August. Gurney and Lebour (1941) described the last larval stage of a shrimp doubtfully referred to *P. wilsoni*.

When disturbed, the animals are able to make a snapping sound with the large chela quite as loud as that made by one of the true snapping shrimps.

Genus *Pontonia* Latreille, 1829

Holthuis, 1951a, p. 115.—Hemming, 1958b, p. 124.

Pontonia domestica Gibbes

Figure 39

Pontonia domestica Gibbes, 1850, p. 196.—Holthuis, 1951a, p. 122, pl. 38, figs. a–j (rev.).

Recognition characters.—Rostrum depressed, rather narrowly triangular, decurved; reaching to second article of antennular peduncle; tip acute

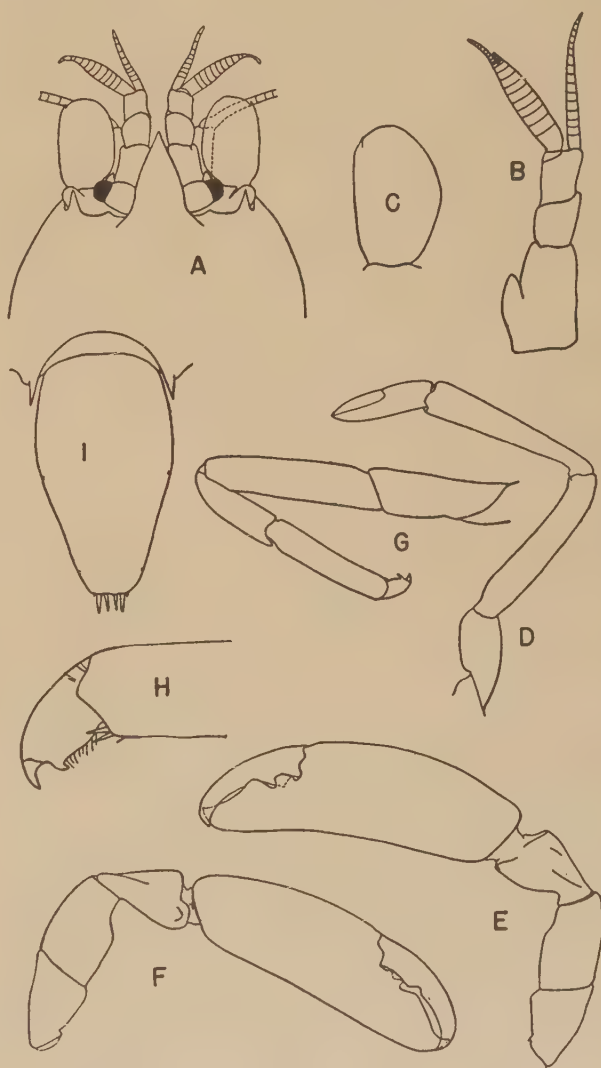


FIGURE 39.—*Pontonia domestica* Gibbes. A, anterior part of body in dorsal view, $\times 5.5$; B, antennule, $\times 7.5$; C, antennal scale, $\times 7.5$; D, first leg, $\times 5.5$; E, larger second leg, $\times 2.5$; F, smaller second leg, $\times 2.5$; G, third leg, $\times 5.5$; H, dactyl of third leg, $\times 20$; I, telson in dorsal view, $\times 9.1$ (after Holthuis, 1951a).

in dorsal and lateral view, flat dorsally; an inconspicuous longitudinal carina ventrally; an inconspicuous dorsal and ventral tooth near tip with tuft of long hairs between upper tooth and apex. Carapace with lower orbital angle bluntly triangular, a strong antennal spine below angle; anterolateral angle broadly rounded and anteriorly produced. Eyes well developed, not reaching laterally to antennal spine. Antennular peduncle with stylocerite broad, bluntly pointed; anterolateral angle of basal article produced forward, rounded; third article longer than second; upper antennular flagellum with 7-10 fused joints; short ramus with 2 or 3 joints. Antennal scale broadly oval, outer margin a little convex, terminal tooth small, exceeded by lamella; antennal peduncle reaching beyond middle of scale.

First leg with carpus and chela reaching beyond antennal scale; fingers of chela somewhat longer than palm; carpus as long as merus. Second legs strong, unequal in size and shape; carpus and chela reaching beyond antennal scale. On one leg, fingers about half length of palm; immovable finger somewhat higher than dactyl and bearing two large teeth on cutting edge, anterior tooth triangular, at middle of edge, posterior tooth truncate with crenulate margin; dactyl with one tooth; palm with upper and lower margin somewhat compressed, surface appearing minutely roughened under magnification; carpus short, conical, with a depression above and a knob below; merus a little longer than carpus. Other second leg much as above but with relatively longer fingers; immovable finger higher in comparison to dactyl; teeth smaller and carpus more slender. Remaining legs with bifurcate dactyls.

Abdomen with first five pleura broadly rounded. Sixth segment with pleura and posterolateral angle ending in slender, sharp spines; slightly longer than fifth segment. Telson half again as long as fifth segment; two dorsal pairs of spines on lateral margin of telson small, almost invisible; anterior pair about in middle, posterior pair closer to posterior border than to anterior pair; posterior border with three pairs of spines in a row; inner two pairs equal in length, outer pair smaller; uropods broadly ovate, outer margin of exopod ending in blunt angle with small movable spine at tip.

Measurements.—Length of body: male 32 mm.

Color.—Translucent white.

Habitat.—The species lives commensally in lamellibranch mollusks in coastal waters and has been recorded from *Atrina seminuda*, *A. serrata*, and *Pecten* sp. (Holthuis, 1951a); shallow water to 23 fathoms.

Type locality.—South Carolina.

Known range.—Atlantic Beach near Beaufort Inlet, N.C., to Chandeleur Islands, La.; Bahamas; Madeira.

Remarks.—Brooks and Herrick (1892) illustrated a section through the segmenting egg of *Pontonia domestica* on plate 28.

Pontonia margarita Smith

Figure 40

Pontonia margarita Smith, 1869c, p. 245.—Holthuis, 1951a, p. 137, pl. 43, figs. a-i; pl. 44, figs. a-h (rev.).

Recognition characters.—Rostrum depressed and decurved, dorsally flat and triangular; tip reaching to end of basal article of antennular peduncle or slightly beyond; an inconspicuous dorsal and ventral tooth near tip with small tuft of hairs between upper tooth and apex; a longitudinal median carina ventrally. Carapace smooth; with strong antennal spine located well below narrowly rounded lower orbital angle; anterolateral angle broadly rounded and anteriorly produced. Eyes somewhat larger than in *P. domestica*, reaching laterally beyond antennal spine. Basal article of antennular peduncle with blunt-pointed stylocerite more or less pressed against outer border; anterolateral angle of article produced forward, rounded; upper antennular flagellum short, thick, curved backward; fused part with six or seven joints; short ramus with two joints. Antennal scale with convex outer margin ending in small inwardly curved distal tooth, lamella far exceeding tooth.

First leg with half or more than half of carpus reaching beyond antennal scale; fingers longer than palm, unarmed; carpus longer than merus. Second legs unequal in size but similar in shape. Larger leg with fingers a little over half length of palm; palm twice as long as deep, somewhat inflated; dactyl narrower than immovable finger and bearing one large tooth slightly behind middle; cutting edge of immovable finger with two large teeth fitting on each side of opposed dactylar

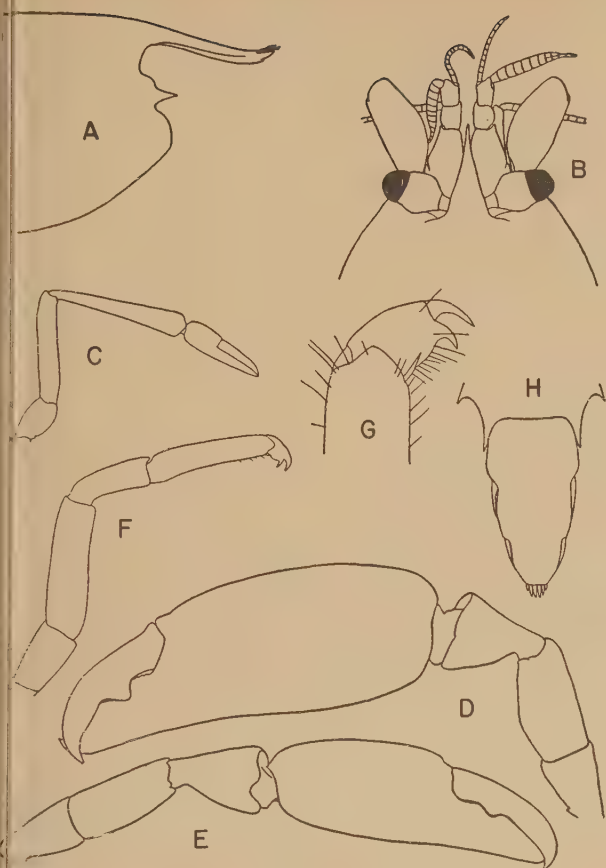


FIGURE 40.—*Pontonia margarita* Smith. A, anterior part of carapace in lateral view, $\times 11.5$; B, anterior part of body in dorsal view, $\times 11.5$; C, first leg, $\times 5.9$; D, larger second leg, $\times 6$; E, smaller second leg, $\times 6$; F, third leg, $\times 9.5$; G, dactyl of third leg, $\times 35$; H, telson in dorsal view, $\times 11.5$ (after Holthuis, 1951a).

both and separated by a hole on inner side of edge, posterior tooth with denticles at apex; carpus shorter than merus, conical. Smaller second leg resembling larger except for relatively longer fingers. Dactyls of last three walking legs bifurcate.

Abdomen with pleura of first five segments broadly rounded, of sixth ending in a strong spine overlapping base of uropods. Sixth segment a little more than half length of telson. Telson with two pairs of large dorsal spines placed laterally, and at one-third and two-thirds of length; posterior border with three pairs of spines in a row, inner two pairs equal, outer pair smaller. Uropods broadly ovate, exopods ending in a minute movable spine on outer margin.

Measurements.—Length of body: male, 19 mm.; ovigerous females, 17 to 27 mm.

Color.—Glassy, translucent; internal organs clearly visible; ovigerous females with two colors of eggs, one with light, muddy green eggs and ovarian ova of same color, another with pale orange eggs (from specimens taken in *Aequipecten gibbus* off Drum Inlet, N.C., in 20-fathom water, April 14, 1960).

Habitat.—The species lives commensally in lamellibranch mollusks in coastal waters. It has been found in *Aequipecten gibbus* and *Pteria colymbus* in North Carolina, and in the pearl oyster *Pinctada fimbriata* on the west American coast; tidal flats to 33 fathoms.

Type locality.—Bay of Panama.

Known range.—Atlantic coast: Drum Inlet to Beaufort Inlet, N.C.; east and west Florida. Pacific coast: Gulf of California to Colombia; Galapagos Islands.

Remarks.—Ovigerous females have been taken in North Carolina in January and April.

Genus *Neopontonides* Holthuis, 1951

Holthuis, 1951a, p. 189.

Neopontonides beaufortensis (Borradaile)

Figure 41

Periclimenes beaufortensis Borradaile, 1920, p. 132.

Neopontonides beaufortensis: Holthuis, 1951a, p. 190, pl. 59, figs. g–k; pl. 60, figs. a–k (rev.).

Recognition characters.—Rostrum slender, straight; a little shorter than antennular peduncle; laterally compressed but broadened at base, covering eyestalks, lateral margin of widened base not merging with orbital margin; upper margin with none to five teeth, most proximal teeth, when present, in front of posterior margin of orbit on a crest, crest remaining visible in absence of teeth; lower margin unarmed. Carapace smooth or somewhat areolated; anterior margin of carapace with lower angle of orbit produced in a rounded lobe; antennal spine strong, located considerably below orbit; a rounded lobe slightly below antennal spine followed by an emargination ending in a produced anterolateral angle; hepatic and supraorbital spines absent. Eyes large, reaching almost to end of rostrum. Basal article of antennular peduncle with sty-

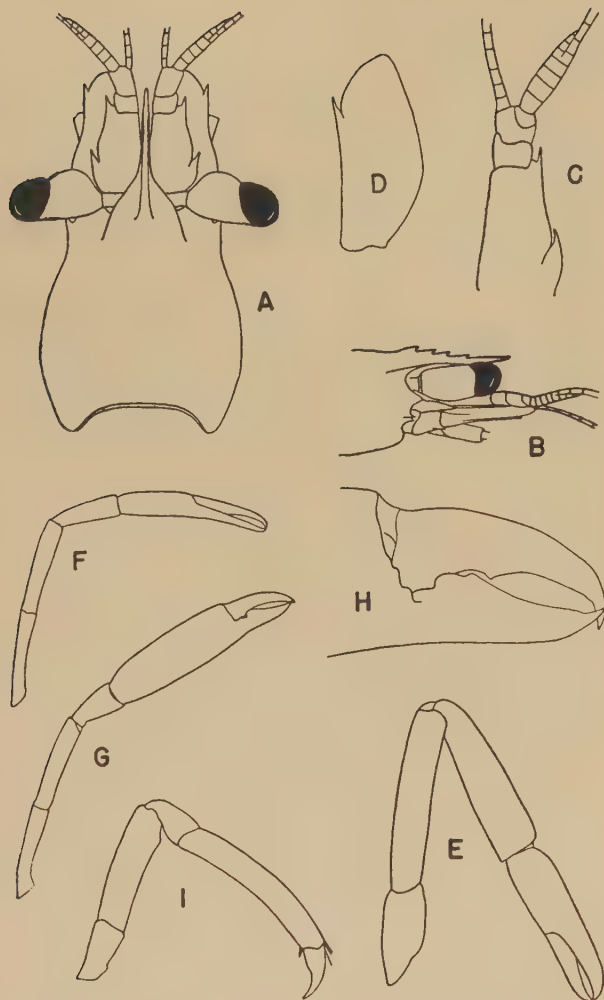


FIGURE 41.—*Neopontonides beaufortensis* (Borradaile). A, anterior part of body in dorsal view, $\times 19.5$; B, anterior part of body in lateral view, $\times 13$; C, antennule, $\times 26$; D, antennal scale, $\times 26$; E, first leg, $\times 39$; F, smaller second leg, $\times 26$; G, larger second leg, $\times 26$; H, fingers of larger second leg, $\times 65$; I, third leg, $\times 26$ (after Holthuis, 1951a).

locerite rather broad, ending in slender point reaching almost to middle of article; outer margin of article slightly concave ending in strong anterolateral spine reaching end of second article; upper antennular flagellum with rami fused for two to four joints; short ramus with two to four free joints. Antennal scale reaching beyond antennular peduncle; concave outer margin ending in strong tooth; lamella exceeding tooth; a small lateral tooth at base; antennal peduncle reaching about to middle of scale.

First leg reaching beyond end of antennal scale; fingers slightly shorter than palm, unarmed, slightly agape; carpus about as long as merus. Second legs unequal. Part of palm of larger leg exceeding antennal scale; fingers half or less length of palm, dactyl with two, immovable finger with one tooth on cutting edge; palm slightly swollen; carpus short, conical; merus about twice length of carpus. Smaller second leg with fingers as long as palm, slender, unarmed; carpus nearly as long as palm. Third leg with heavy, simple dactyl.

Abdomen smooth, all pleura broadly rounded. Sixth segment as long as telson. Telson with two pairs of dorsolateral spines; posterior pair midway between anterior pair and tip; three pairs of spines on posterior border, intermediate pair less than twice length of inner pair. Uropods elongate; outer margin of exopod ending in a tooth flanked medially by a movable spine.

Measurements.—Length of body: male, 9 mm.; ovigerous females, 7 to 9 mm.

Variations.—In young specimens, the legs are relatively shorter than in adults, and the larger second leg resembles the smaller second leg of adults.

Color.—Nearly transparent, but with faint coloration of *Leptogorgia* from which individuals are taken (yellow or orange).

Habitat.—This species is found in coastal waters where it lives in association with *Leptogorgia*; surface to a few fathoms.

Type locality.—Beaufort, N.C.

Known range.—Beaufort, N.C., to Grand Isle, La. (Dawson, 1963); Caledonia Bay, Panama; Antigua.

Remarks.—Ovigerous females have been taken in Bogue Sound near Beaufort Inlet, N.C., in August and November, in Panama in April, and in Antigua in May.

Subfamily Palaemoninae

Upper antennular flagellum with both rami fused in basal part. Appendix masculina generally present on second pleopod of male, appendix interna on second pleopod of female. Pleurobranch present on third maxilliped. Posterior margin of telson with two pairs of spines and one or more pairs of setae (Holthuis, 1952).

KEY TO GENERA AND SPECIES IN THE CAROLINAS

(Holthuis, 1952, modified)

- a. Hepatic spine present, branchiostegal spine absent; chelate second legs enlarged and greatly elongated.
- b. Dactyls of last three legs bifurcate; marine

Brachycarpus biunguiculatus (p. 51).

- bb. Dactyls of last three legs simple; fresh or brackish water-----*Macrobrachium* (p. 52).

- c. Fingers of chelae on second legs thickly pubescent throughout length; rostrum with teeth extending up to tip-----*M. acanthurus* (p. 52).

- cc. Fingers of chelae on second legs with scattered hairs, except thicker on fingers along cutting edges; rostrum with toothless daggerlike tip

M. ohione (p. 54).

- aa. Hepatic spine absent, branchiostegal spine present; chelate second legs not greatly enlarged.

- b. Mandible with a palp---*Leander tenuicornis* (p. 55).

- bb. Mandible without a palp---*Palaemonetes* (p. 56).

- c. Carpus of second leg in adult female shorter than palm, in males slightly longer or shorter (1.1 times) than palm; dactyl of second leg with two, immovable finger with one tooth on cutting edge; rostrum with first two teeth of dorsal margin behind orbit, dorsal rostral teeth reaching to apex, lower margin with three to five teeth

P. vulgaris (p. 56).

- cc. Carpus of second leg in adult female much longer than palm (1.3 to 1.5 times), in males almost as long as whole chela; dactyl of second leg with a single tooth or without teeth, immovable finger without teeth on cutting edge; rostrum with only one dorsal tooth behind orbit.

- d. Dorsal teeth of rostrum reaching up to apex, apex often bifurcate; lower margin of rostrum with four or five, seldom three teeth; dactyl of second leg with one distinct tooth on cutting edge -----*P. intermedius* (p. 58).

- dd. Dorsal and ventral margins of rostrum with an unarmed stretch before dagger-shaped tip; lower margin of rostrum with two to four, generally three, teeth; fingers of second leg without teeth on cutting edges-----*P. pugio* (p. 59).

Genus *Brachycarpus* Bate, 1888

Holthuis, 1952, p. 2.—Hemming, 1958b, p. 154.

Brachycarpus biunguiculatus (Lucas)

Figure 42

Palaemon biunguiculatus Lucas, 1849, p. 45, pl. 4, fig. 4.

Brachycarpus biunguiculatus: Holthuis, 1952, p. 3, pl. 1, figs. aa-q (rev.).

Recognition characters.—Rostrum well developed, rather high, directed straight forward, reaching about to end of antennal scale; upper margin with seven (seldom eight) teeth, first two teeth placed behind orbit with first tooth at about

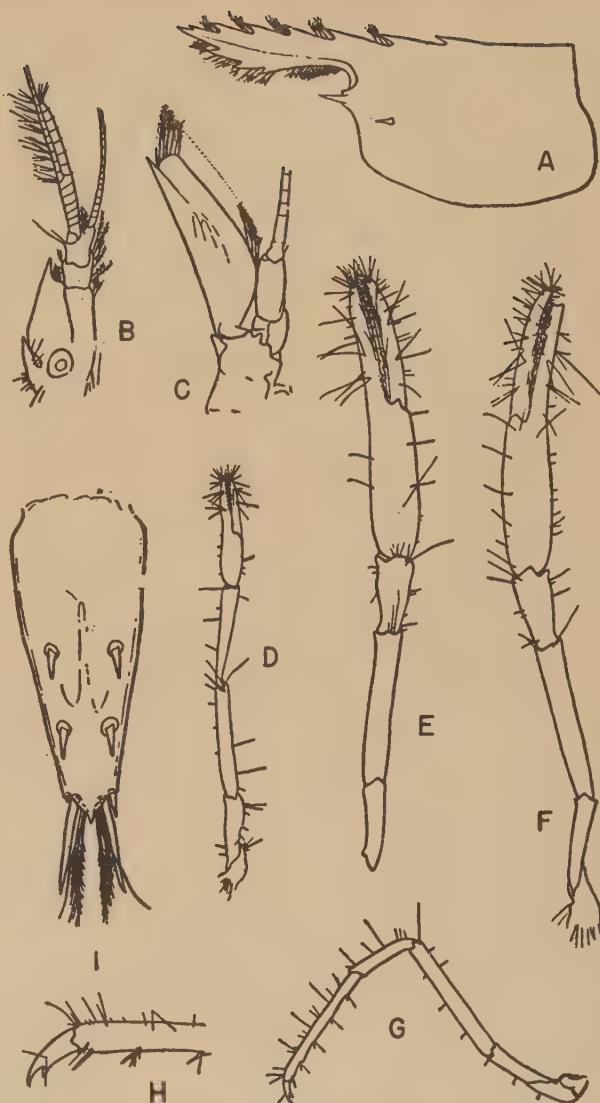


FIGURE 42.—*Brachycarpus biunguiculatus* (Lucas). A, carapace in lateral view, $\times 6$; B, antennule, $\times 7$; C, antenna, $\times 7$; D, first leg, $\times 6$; E, left second leg, $\times 6$; F, right second leg, $\times 6$; G, third leg, $\times 6$; H, dactyl of third leg, $\times 16$; I, telson, $\times 15$ (after Schmitt, 1939).

midlength of carapace; lower margin with three (seldom two or four) teeth. Carapace smooth; antennal and hepatic spines present; a strong postorbital ridge paralleling orbit. Eyes well developed. Basal article of antennular peduncle with anterolateral spine strong, reaching beyond second article of peduncle; stylocerite small, acute, closely appressed to article; rami of inner antennular flagellum fused for 8 to 23 joints; free part

of shorter ramus about as long as fused portion. Antennal scale about three times longer than broad, outer margin concave, terminal spine overreaching lamella.

First legs slender; fingers of chelae longer than palm; carpus longer than chela. Second legs much stronger than first; smooth; part of carpus extending beyond antennal scale; fingers slightly shorter than palm, but in adult males sometimes only half length of palm, cutting edge of dactyl with two to four, immovable finger with two small teeth in proximal part, adult males with fingers widely agape, opening hairy; carpus short, cup-shaped, half length of merus. Last three legs slender, dactyls bifurcate, propodi with spines present on posterior margin.

Abdomen smooth, pleura of fourth and fifth segments pointed. Telson with two pairs of dorsal and two pairs of posterior spines; numerous setae between inner posterior spines. Appendix interna present on first pleopods in males, missing in females.

Measurements.—Length of body: 65 mm. (Holthuis, 1952).

Variations.—Dorsal spines on the telson are sometimes not placed in symmetrical pairs and may be asymmetrically doubled.

Color.—Living individuals: body dark blue green mottled with white; palm of chela uniform blue green, fingers barred; fringes of antennules, antennae, antennal scale and tail fan orange; some individuals colorless, with tawny-tinged spots. Preserved specimens: pale brownish yellow, tips of fingers brownish red preceded by colorless band, then a fainter band of brownish red; antennular flagella red with white rings at articulations between joints (Holthuis, 1952).

Habitat.—Found near shore among corals or rocks, and on sea buoys; surface to 4 fathoms.

Type locality.—Oran and Bône, Algeria.

Known range.—Virtually pantropical; East and West American coasts, Mediterranean; West Africa; and Indo-Pacific region. Western Atlantic distribution: Cape Fear, N.C., through West Indies to Curaçao and Old Providence Island; Bermuda.

Remarks.—Gurney and Lebour (1941) described a complete series of 11 larval stages and

a postlarval stage of this species from Bermuda. They pointed out that the larval life of this form may be indefinite in length and number of developmental stages, and that this feature of development may account for the wide distribution of the species. Gurney (1943a) noted proportional changes in growth of the segments of the second legs in the last larval stage, first postlarval stage, and adult female.

Genus *Macrobrachium* Bate, 1888

Holthuis, 1952, p. 10.

Macrobrachium acanthurus (Wiegmann)

Figures 43-44

Palaemon acanthurus Wiegmann, 1836, p. 150.

Macrobrachium acanthurus: Holthuis, 1952, p. 45, pl. 9, figs. a-b (rev.).

Recognition characters.—Rostrum almost straight, reaching slightly beyond antennal scale; upper margin slightly arched basally, with 9-11 teeth, proximals closer together than distals, first 2 teeth on carapace behind orbit, second tooth sometimes partly over posterior margin of orbit and separated from first tooth by distance greater than that between other proximal teeth; lower margin with 4 to 7 (generally 6) teeth, proximals closer together than distals. Carapace smooth, with short hairs especially on anterolateral region; antennal spine a little below orbit and slightly removed from margin; hepatic spine behind and a little below antennal spine. Antennal scale about three times longer than broad; outer margin straight or convex.

First legs with chela and sometimes part of carpus reaching beyond scale; fingers as long as palm; carpus one-third longer than merus. Second legs equal, with carpus and sometimes part of merus reaching beyond scale; fingers slender, thickly pubescent throughout length, slightly shorter than palm, cutting edges with a tooth on each finger in proximal quarter (that of dactyl more advanced) preceded by row of about four denticles; palm elongate, cylindrical, with several longitudinal rows of spinules largest and widest apart on inner and lower regions; carpus and merus spinulose like palm. Articles of last three walking legs with numerous densely placed small spinules.



FIGURE 43.—*Macrobrachium acanthurus* (Wiegmann). Animal in lateral view (after Hedgpeth, 1949).

Abdomen smooth; pleura of fifth segment ending in an acute point. Telson 1.5 times length of sixth segment, with pairs of dorsal spines at middle and three-fourths of length; posterior margin ending in sharp median point flanked by two pairs of spinules, inner pair overreaching median point.

Measurements.—Length of body: male, 166 mm.; ovigerous females, 36 to 110 mm.

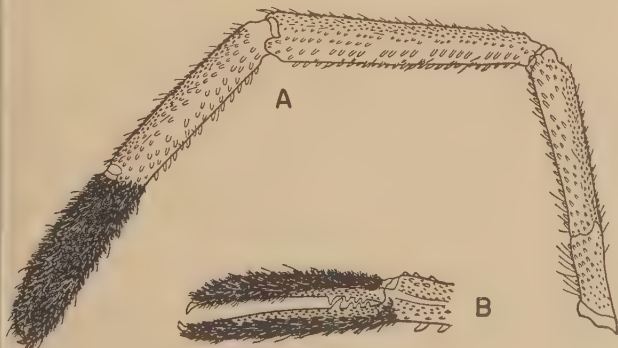


FIGURE 44.—*Macrobrachium acanthurus* (Wiegmann). A, second leg of adult male; B, fingers of second leg of adult male (part of hairs removed); A, B, $\times 0.75$ (after Holthuis, 1952).

Variations.—The rostrum may vary in length and shape. Adult females and young males have second legs shorter, more slender, less spinulose and pubescent than adult males.

Color.—Green or pale yellow with red speckles; carapace with middorsal stripe of red or brownish orange and occasionally with irregular red bands laterally; chelipeds greenish becoming blue distally, articulations orange; abdomen with mid-dorsal stripe similar to carapace, pleura green with blue edges and striped with red; eggs green (Hedgpeth, 1949; Schmitt in Holthuis, 1952).

Habitat.—The species lives in coastal rivers and bays, usually near brackish water, but sometimes quite far upstream; 97 miles from mouth of Rio Grande River in Texas (Hedgpeth, 1949).

Type locality.—Brazilian coast.

Known range.—Neuse River estuary, N.C., to Rio Grande do Sul, Brazil; West Indies.

Remarks.—This species probably has a later breeding season than *Macrobrachium ohione* (Hedgpeth, 1949). The recent discovery of *M. acanthurus* in the Neuse River estuary of North Carolina may indicate an active northward extension of range similar to the case of *M. ohione*.

Macrobrachium ohione (Smith)

Figure 45

Palaemon Ohionis Smith, 1874, p. 640.

Macrobrachium ohione: Holthuis, 1952, p. 62, pl. 14, fig. b (rev.).

Recognition characters.—Rostrum high and straight, tip curving somewhat upward and reaching to between end of antennular peduncle and end of antennal scale; upper margin with 9 to 13 teeth, 3 or 4 teeth behind orbit, first 3 more widely separated than remainder; lower margin with 1 to 3 teeth; distal two-fifths of rostrum unarmed. Carapace smooth; antennal spine slightly remote from anterior margin; hepatic spine below antennal spine. Antennal scale about 2.5 times longer than broad; outer margin straight or slightly concave.

First legs with chelae reaching beyond scale; chelae slender; fingers about as long as palm; carpus twice length of chela. Second legs in adult female stronger than in male, with carpus and chela reaching beyond scale; fingers somewhat shorter than palm, cutting edges pubescent and

with four to eight small denticles of equal size on proximal half, remainder of surface with scattered hairs; palm elongate, cylindrical, entirely pubescent, most conspicuous pubescence along lower surface; carpus, merus, and palm of equal length, these articles and fingers with longitudinal rows of small spinules; carpus most pubescent anteroventrally; merus somewhat pubescent anteroventrally.

Abdomen smooth; pleura of fifth segment ending in acute point. Telson about 1.5 times length of sixth segment; pairs of dorsal spines at middle and three-fourths of length; posterior margin ending in an acute tip overreached by inner pair of posterior spines.

Measurements.—Length of body: male, 68 mm.; female, 102 mm.

Variations.—Juveniles (10 mm. and larger) have the same number of rostral spines as adults but fewer spines behind the orbit. In such juveniles, the hepatic spine is very close to the anterior margin of the carapace, similar in position to a branchiostegal spine.

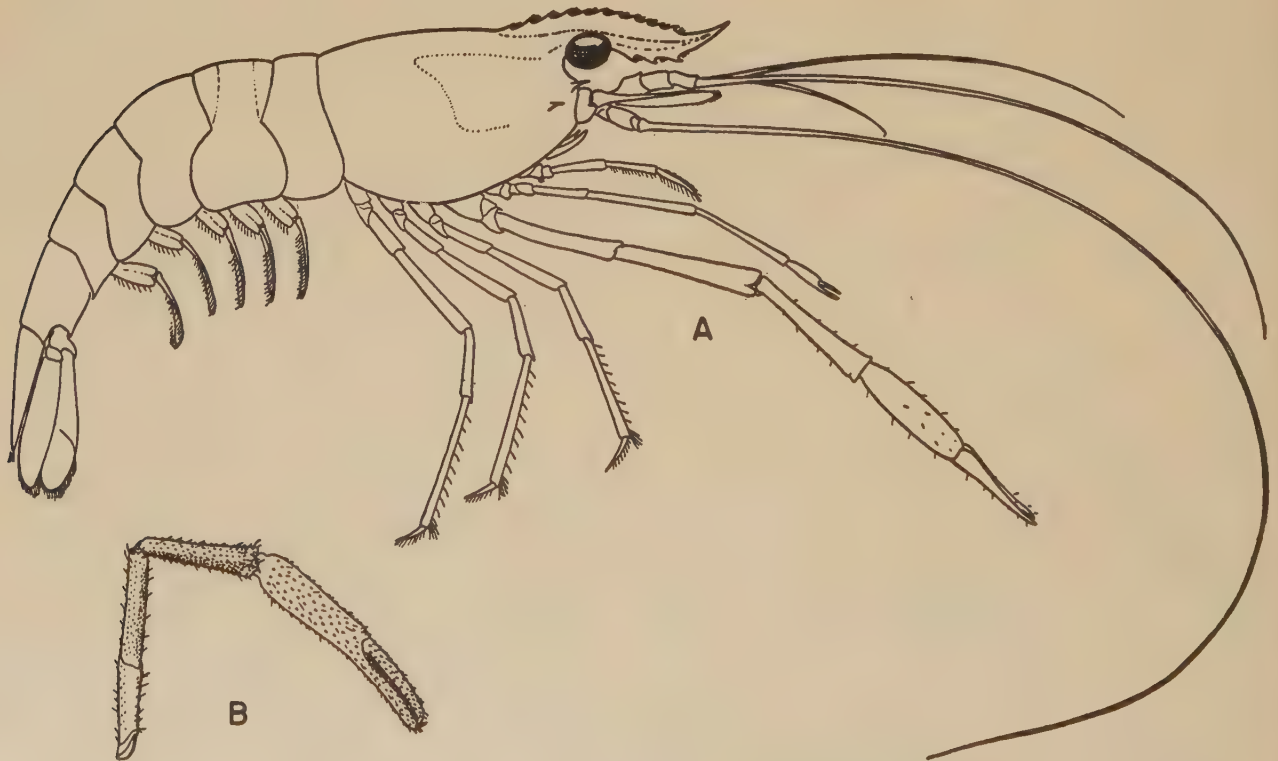


FIGURE 45.—*Macrobrachium ohione* (Smith). A, animal in lateral view (after Hedgpeth, 1949); B, second leg of adult male (after Holthuis, 1952).

Color.—Pale gray flecked with small blue spots; uropods pale blue (Hedgpeth, 1949).

Habitat.—This species lives in rivers and estuaries.

Type locality.—Ohio River at Cannelton, Ind.

Known range.—A narrow zone along Atlantic seaboard from James River, Hopewell, Va. (Hobbs and Massmann, 1952), to southern Georgia; widespread from coastal Alabama to Aransas Bay, Tex.; Mississippi River and tributaries upstream to McCurtain County, Okla.; Fort Smith, Ark.; St. Louis, Mo.; Washington County, Ohio.

Remarks.—This species is distributed chiefly in brackish and fresh water, ranging far inland in the Mississippi River drainage. It is abundant enough, especially in Louisiana, to provide a fishery of some importance though the exact magnitude is not known. Gunter (1937) described the Louisiana fishery and gave information on ecology of the species. Commercially, the shrimp are taken in traps made of wooden slats, similar to lobster traps, baited with meat scraps or cottonseed cake. The shrimp are sometimes captured by lifting submerged willow branches from the water and catching the animals as they drop off. Such catches are best made at night. Commercial shrimping is done in the warmer months, as the animals are scarce in winter. The shrimp will attack fish kept in live boxes in the river, and, though the feeding habits of the species are not known completely, the animals are thought to be primarily carnivorous.

During a period of study from November to early July, Gunter found that ovigerous females first appeared in mid-April, and egg-bearing females were still present when the work was terminated in July. Ovigerous females have been found in April and May in North Carolina. McCormick (1934) stated that eggs in various stages of development were found in females at the same time that they were in berry, which indicates a long egg-laying season. Gunter found females to outnumber males by more than 3 to 1. However, this ratio varied. When females were carrying eggs, males made up only 9 percent of the captured individuals, but prior to the egg-laying season males made up 31.8 percent of the total. He concluded that this indicated a change in sex ratio at the egg-bearing period.

Thirteen percent of the females caught were ovigerous, and these ranged in length from 38 to 76 mm. Eggless females ranged from 23 to 93 mm. in length. From November to December, the population was made up of individuals 60–80 mm. long. In January, shrimp below 30 mm. average length predominated, but from then until April the average length increased to about 50 mm., and thereafter the range of variation widened as smaller animals came into the catch.

Gunter found ovigerous females in bay water with salinities ranging from 1.38 to 14.24 ‰. He noted that when the river was on a rise, with turbidity high, few shrimp were taken in water over 20 feet deep, and these were sometimes dead. He conjectured that because these shrimp were not buried in mud, high turbidity in deep water during flood may have an adverse effect on respiration. Hedgpeth (1949) suggested that silt causing interference with respiration may drive the shrimp from rivers to estuaries during such seasons, but he also suggested that in regions such as the Atlantic seaboard, where the species is apparently a comparatively recent immigrant, it may still depend on bay waters to complete its breeding cycle. In any case, it is thought that these shrimp and other species of the genus move from river to river through the salty estuaries at the river mouths (Gunter, 1937).

Especially interesting is the fact that this species and *M. acanthurus* are forms which may be advanced in the process of moving from the sea to fresh water. Few such examples exist.

Genus *Leander* Desmarest, 1849

Holthuis, 1952, p. 167.

Leander tenuicornis (Say)

Figure 46

Palaemon tenuicornis Say, 1818, p. 249.—Hay and Shore, 1918, p. 392, pl. 27, fig. 6.

Leander tenuicornis: Holthuis, 1952, p. 155, pl. 41, figs. a–g; pl. 42, figs. a–f (rev.).

Recognition characters.—Rostrum well developed; high in female, more slender in male; reaching about to end of antennal scale; upper margin with 8 to 14 regularly spaced teeth, first two behind orbit; lower margin with 5 to 7 teeth partially concealed by double row of setae. Carapace smooth; antennal spine present, and a branchiostegal spine placed some distance behind anterior margin; branchiostegal groove absent.

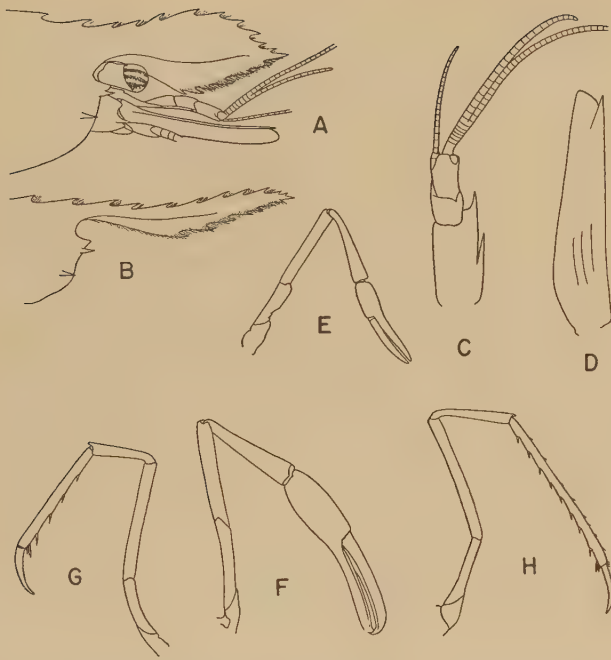


FIGURE 46.—*Leander tenuicornis* (Say). A, anterior part of body of female in lateral view; B, anterior part of carapace of male in lateral view; C, antennule; D, antennal scale; E, first leg; F, second leg; G, third leg; H, fifth leg (after Holthuis, 1952).

Eyes well developed, rounded; two dark-colored bands visible on cornea, especially in fresh material. Basal article of antennule with stylocerite large and pointed, reaching beyond middle of article, and with anterolateral spine reaching almost to end of second article of peduncle, anterior margin of basal article between spine and second article straight or only slightly convex; second and third antennular articles shorter and narrower than first; upper flagellum with fused portion of rami shorter than free portion of shorter ramus. Antennal scale 3 to 5 times longer than broad; outer margin about straight; terminal tooth strong, as long as lamella; antennal peduncle not reaching middle of scale; a strong external spine near base of scale. Mandible with a two-jointed palp.

First pair of legs slender; reaching about to end of scale; fingers longer than palm. Second legs more robust than first, equal in size and shape; chelae reaching beyond scale; fingers longer than slightly swollen palm, cutting edges of fingers entire except for small basal tooth in males; carpus shorter than chela and about as

long as merus. Last three legs slender, dactyls simple, slender; propodi armed with posterior spinules; fifth leg more slender than third.

Abdomen smooth; first three pleura broadly rounded; pleura of fourth and fifth segments narrower, ending in a minute, acute tooth. Sixth segment slightly longer than fifth and about two-thirds length of telson. Telson with two pairs of dorsal spines, first pair at midlength, second at three-fourths length; inner of two pairs of posterior spines overreaching acute tip of telson, a pair of strong feathered setae between inner pair of spines.

Measurements.—Length of body: 47 mm.; males generally smaller than females; ovigerous females 26 mm. long have been reported (Holthuis, 1952).

Variations.—Length of the second legs is variable, and the palm of the chela is more swollen in some specimens than in others. Length of the terminal tooth of the antennal scale is variable.

Color.—Green or olive, with opaque spots (Schmitt in Holthuis, 1952, for specimens from Tortugas).

Habitat.—Found in floating sargassum, on wharf pilings, and among submerged vegetation.

Type locality.—Newfoundland Banks.

Known range.—Tropical and subtropical waters all over world except for west coast of Americas; Newfoundland Banks to Falkland Islands in western Atlantic (Holthuis, 1952).

Remarks.—Ovigerous females have been observed from July to October in the Carolinas, in June in the middle and western Atlantic (Sivertsen and Holthuis, 1956), and in August at Old Providence Island (Schmitt, 1939). Gurney (1939) described the fifth(?) larval and first postlarval stages and compared them to related forms, with remarks on the statocyst in adults.

Genus *Palaemonetes* Heller, 1869

Holthuis, 1952, p. 199. Hemming, 1958b, p. 158.

Subgenus *Palaemonetes* Heller

Holthuis, 1952, p. 207.

Palaemonetes (*Palaemonetes*) *vulgaris* (Say)

Figure 47

Palaemon vulgaris Say, 1818, p. 248.

Palaemonetes carolinus: Hay and Shore, 1918, p. 393, pl. 27, fig. 4.

Palaemonetes (*Palaemonetes*) *vulgaris*: Holthuis, 1952, p. 231, pl. 54, figs. f-1 (rev.).

Recognition characters.—Rostrum reaching to or slightly beyond end of antennal scale; tip directed upward making upper margin more or less concave; upper margin with 8 to 11 teeth, first 2 teeth behind orbital margin and separated more widely than other proximal teeth, all teeth rather regularly distributed along rostrum but proximals generally closer together than distals, no unarmed space behind tip, tip often bifurcate; lower margin with 3 to 5 (usually 4) teeth. Carapace smooth; antennal spine present; branchiostegal spine on anterior margin just below branchiostegal groove. Eyes well developed. Basal article of antennular peduncle with slender stylocerite reaching slightly beyond middle of article, anterolateral spine of article strong, overreaching rounded anterior margin; upper antennular flagellum with both rami fused for 7 to 9 joints; free part of shorter ramus with 10 to 17 joints, at least 1.5 times as long as fused portion. Antennal scale 3 times longer than broad; terminal tooth strong, reaching almost to end of lamella.

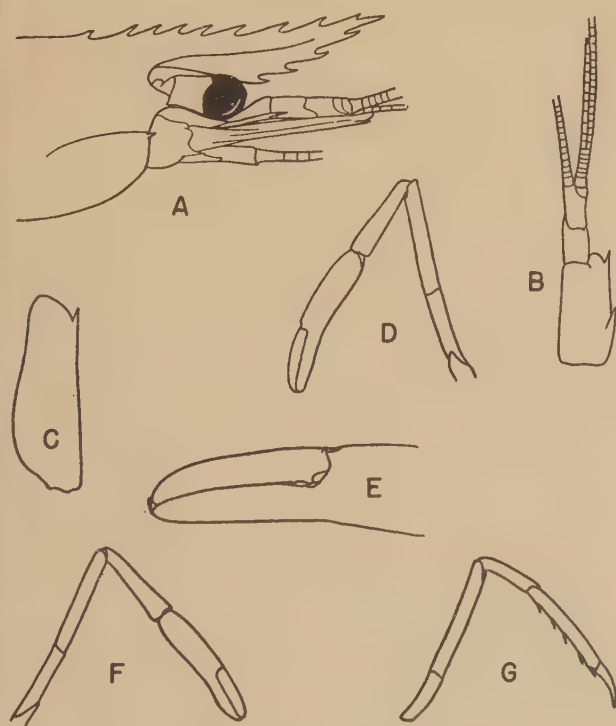


FIGURE 47.—*Palaemonetes* (*Palaemonetes*) *vulgaris* (Say). A, anterior part of body in lateral view; B, antennule; C, antennal scale; D, second leg of female; E, fingers of second leg of female; F, second leg of male; G, third leg; A–G $\times 5$ (after Holthuis, 1952).

First leg usually not reaching to end of antennal scale; fingers about as long as palm; carpus 1.3 to 1.7 times as long as chela and a little longer than merus. Second legs longer and stronger than first, stronger in adult females than in males with fingers and sometimes entire palm reaching beyond scale; fingers a little over half length of palm, cutting edge of dactyl with two small teeth proximally, immovable finger with one similar tooth fitting between those of dactyl; carpus shorter than palm and about three-fourths length of merus. Second legs of male not so large as in female; teeth on fingers indistinct. Third leg with propodus less than twice length of carpus. Fifth leg with propodus about three times length of dactyl, twice as long as carpus.

Abdomen smooth; fifth segment with tip of pleura rectangular or slightly acute. Sixth segment 1.5 times length of fifth, shorter than telson. Telson with two pairs of dorsal spines; anterior pair somewhat behind middle; second pair halfway between these and tip; posterior margin with strong median point flanked by two pairs of spines, inner pair longest and between them two feathered setae. Outer margin of uropodal exopod with a strong terminal tooth flanked by a slender movable spine medially.

Measurements.—Length of body: male, 30 mm.; ovigerous females, 22 to 42 mm.

Color.—Transparent in life.

Habitat.—Estuarine waters, especially in beds of submerged vegetation; water's edge to (rarely) 8 fathoms. Salinity of 3‰ is apparently lethal (Nagabhushanam, 1961).

Type locality.—Atlantic coast of United States.

Known range.—Barnstable County, Mass., to Cameron County, Tex. (from specimens examined by Holthuis, 1952). Literature records: Gaspé, Quebec, Canada, to Rio Champoton and near Progreso, Yucatan, Mexico (Holthuis, 1952).

Remarks.—Correct identification of the species of *Palaemonetes* occurring on the east coast of the United States was not possible until Holthuis (1949) introduced his key. As Holthuis (1952) pointed out, two names, *vulgaris* and *carolinus*, were applied indiscriminately to three species but the description of *carolinus* was actually based on a specimen of *vulgaris*; hence, this name is a synonym of *vulgaris*. With the status of *vulgaris* stabilized, Holthuis went on to show that two

other closely related and newly described species, *intermedius* and *pugio*, occupy much the same habitat and geographic range as *vulgaris*. An unfortunate but natural result of such confusion is that the voluminous literature on "*vulgaris*" undoubtedly concerns all three species in unknown ways, and all such literature must now be viewed with reserve.

Jenner (1955) showed that in the Woods Hole, Mass., region, where much of the experimental work on *Palaemonetes* has been done, both *P. vulgaris* and *P. pugio* occur. He showed that a useful field character for differentiating these two species is color of the eyestalks, the eyestalks of *P. pugio* being generally much more yellow than those of *P. vulgaris*, the latter being more red brown. The source of *Palaemonetes* for the Marine Biological Laboratory is thought to have been principally from the dock where only *P. vulgaris* has been found; hence, Jenner suggested that most of the experimental work at Woods Hole has been correctly referred to *P. vulgaris*. In North Carolina, these eye-color differences are less apparent.

The breeding season for the species in Virginia and the Carolinas extends from April to mid-October. Larval stages of *P. vulgaris* have been described by Broad (1957a) and are summarized below under the account for *P. pugio*.

Burkenroad (1947a) showed that male *P. vulgaris* respond only to females which have molted to breeding form recently. After mating, the female resists further courtship. Males recognize such females only upon contact of the antennae with any surface of the female. The spermatophore will adhere to any part of the integument of either sex, but becomes nonadhesive almost immediately after exposure. Burkenroad stated that the sperm-bearing matrix of the spermatophore dissolves about a half hour or less before spawning, and he thought that some substance freeing the sperm cells must be released by the female at the approach of spawning.

Eggs are released simultaneously from both oviducts in a continuous stream. Fertilization is external and, because sperm cells of decapod crustaceans in general are nonmotile, it was suggested that entry of the sperm cell precedes development of the egg membranes in all decapods.

All parts of the eggshell are produced by the ovum or the embryo. The first membrane is developed upon contact with water. The second is developed about half an hour after spawning, and the third about 12 hours after spawning in fertile eggs only. The fourth and last membrane is an embryonic molt skin.

In *Palaemonetes*, the eggs are not adhesive when laid and first adhere to each other about half an hour after spawning. No attachment surface other than the first membrane of the egg develops. The eggs become fused, apparently by their own membranes, to the special setae in the brood pouch of the female. Egg stalks are drawn out by stretching movements of the pleopods. It is possible that the membrane is activated to become adhesive by the secretion of an enzymelike material released among the eggs by the mother from the pleopodal glands during attachment. Only near sources of this secretion would such attachment occur; therefore, the eggs usually do not stick to each other but rather to the setae.

Since the early 1930's much experimental work has been done on the endocrine system in relation to color control in *Palaemonetes* assumed to be *vulgaris*. The shrimp has been found to have four kinds of pigment under independent hormonal control—red, yellow, white, and blue. These pigments are mediated through the eyes by the background on which the animal is found. The source of the hormones is principally the sinus gland in the eyestalk and the central nervous organs (Brown, 1933, 1935a, 1935b, 1948; Brown, Fingerman, and Hines, 1952; Brown, Hines, and Fingerman, 1952; Brown, Webb, and Sandeen, 1952). Persons interested are referred to the source material, for the conclusions are too detailed for adequate summary here.

Palaemonetes (Palaemonetes) intermedius Holthuis

Figure 48

Palaemonetes (Palaemonetes) intermedius Holthuis, 1949, p. 94, fig. 2, j-1.—Holthuis, 1952, p. 241, pl. 55, figs. a-f (rev.).

Recognition characters.—Rostrum reaching to or somewhat beyond end of antennal scale, tip directed upward making upper margin more or less concave; upper margin with 7 to 10 (usually 8 or 9) teeth, first tooth placed behind orbital margin, second tooth before or just over posterior orbital margin; teeth rather evenly divided over

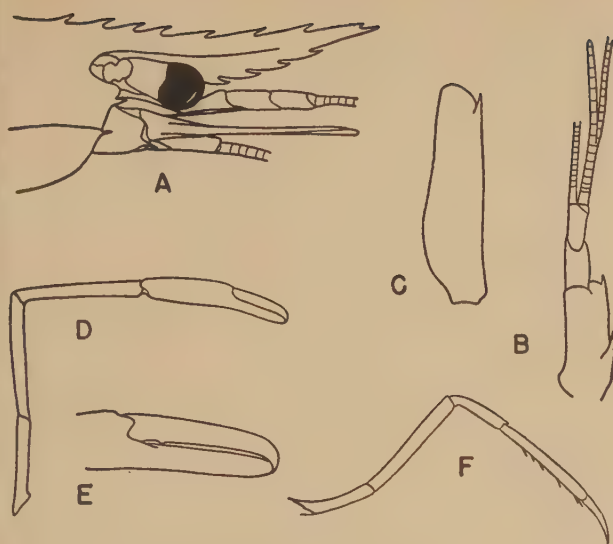


FIGURE 48.—*Palaemonetes (Palaemonetes) intermedius* Holthuis. A, anterior part of body in lateral view; B, antennule; C, antennal scale; D, second leg of female; E, fingers of second leg of female; F, third leg; A–F $\times 4.75$ (after Holthuis, 1952).

dorsal margin up to often bifurcate tip, distal teeth more widely spaced than proximals; lower margin with 4 or 5 (occasionally 3) teeth. Carapace smooth; antennal spine present; branchiostegal spine on anterior margin just below branchiostegal groove. Eyes well developed. Antennular peduncle as in *vulgaris*, basal article with slender stylocerite reaching about to middle of article, anterolateral spine of article strong, overreaching rounded anterior margin; upper antennular flagellum with both rami fused for 7 to 10 joints; free part of shorter ramus with 7 to 12 joints, longer than fused portion. Antennal scale slender, 3 to nearly 4 times as long as broad in females, even more slender in males; outer margin straight or slightly concave; terminal tooth reaching about to end of lamella.

First legs almost reaching tip of antennal scale; fingers as long as palm; carpus twice length of chela and slightly longer than merus. Second legs in adult female usually with almost entire chela reaching beyond antennal scale; fingers a little over half length of palm, cutting edge of dactyl with one proximal tooth, remainder of cutting edges of both fingers entire; carpus 1.2 to 1.5 times length of palm and as long as merus. Second leg of male somewhat more slender than in female; only fingers reaching beyond scale; carpus

as long as merus. Third leg with propodus less than twice as long as carpus. Fifth leg with propodus about three times as long as dactyl, twice as long as carpus.

Abdomen smooth; pleura of fifth segment with tip rectangular or slightly acute; sixth segment 1.5 times length of fifth, somewhat shorter than telson. Telson with two pairs of dorsal spines; anterior pair somewhat behind middle; second pair halfway between these and tip; posterior margin with strong median point flanked by two pairs of spines, inner pair longest and between these, two feathered setae. Outer margin of uropodal exopod with a strong terminal tooth flanked by a slender movable spine medially.

Measurements.—Length of body: male, 30 mm.; ovigerous females, 20 to 42 mm.

Variations.—In males and juveniles, the legs reach less far forward than in ovigerous females (Holthuis, 1952). The second chelae of some females have one tooth on the cutting edge of each finger.

Color.—Transparent in life.

Habitat.—Estuarine waters, especially in beds of submerged vegetation.

Type locality.—Iron Box Bay, Chincoteague Bay, Va.

Known range.—Long Island, N.Y., to Port Aransas, Tex. (from specimens examined by Holthuis, 1952). Literature records: Vineyard Sound to Aransas National Wildlife Refuge, Tex. (Holthuis, 1952).

Remarks.—The confused taxonomic status of this species in literature is discussed in the account for *P. vulgaris* and dealt with in more detail by Holthuis (1952). Ovigerous females have been found from February to April in Texas (Hedgpeth, 1950), and from May to September in Virginia and the Carolinas.

Palaemonetes (Palaemonetes) pugio Holthuis

Figure 49

Palaemonetes vulgaris: Hay and Shore, 1918, p. 393, pl. 27, fig. 5.

Palaemonetes (Palaemonetes) pugio Holthuis, 1949, p. 95, figs. 2, m–o.—Holthuis, 1952, p. 244, pl. 55, figs. g–l (rev.).

Recognition characters.—Rostrum reaching to or slightly beyond end of antennal scale; straight, sometimes slightly upturned at tip; dorsal margin with 7 to 10 (usually 8 or 9) teeth, distal teeth more widely spaced than proximal teeth, first

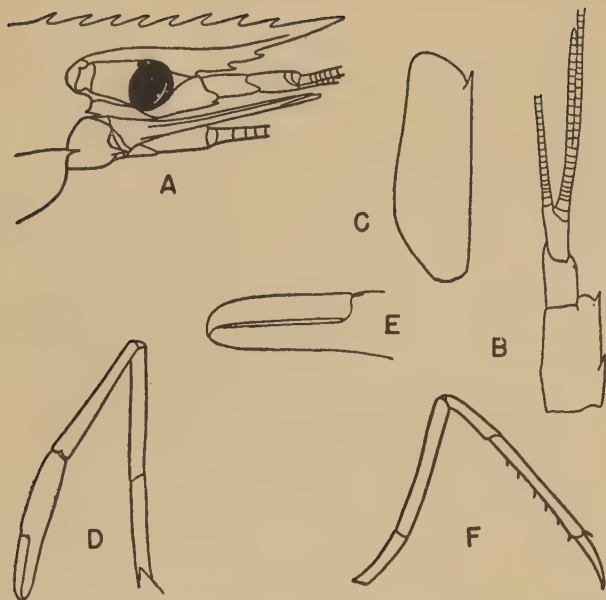


FIGURE 49.—*Palaemonetes (Palaemonetes) pugio* Holthuis. A, anterior part of body in lateral view; B, antennule; C, antennal scale; D, second leg of female; E, fingers of second leg of female; F, third leg; A–F $\times 4.75$ (after Holthuis, 1952).

tooth placed behind orbital margin, distal tooth placed at a distance from tip leaving space before tip unarmed; lower margin with 2 to 4 (usually 3) teeth, distal tooth also placed at distance from tip, tip dagger shaped. Carapace smooth; antennal spine present; branchiostegal spine on anterior margin just below branchiostegal groove. Eyes well developed. Antennular peduncle as in *vulgaris*; basal article with slender stylocerite reaching slightly beyond middle of article, anterolateral spine of article strong, overreaching rounded anterior margin; upper antennular flagellum with both rami fused for 10 to 14 joints; free part of shorter ramus with 12 to 18 joints, longer than fused portion. Antennal scale 2.5 to 3 times longer than broad (length 3 times breadth in males); outer margin convex; terminal tooth strong, almost reaching end of lamella.

First legs not quite reaching tip of antennal scale; fingers as long as palm; carpus nearly twice length of chela and slightly longer than merus. Second legs stronger than first; in adult female, fingers reaching beyond scale, fingers more than half length of palm, cutting edges of both fingers

with no teeth, often gaping proximally; carpus 1.3–1.5 times length of palm but shorter than entire chela; merus as long as carpus. Male with second legs more slender and shorter than in female; fingers shorter than palm; carpus nearly as long as whole chela and as long as merus. Third legs with propodus twice length of carpus. Fifth leg with propodus about 2 times length of dactyl, 2.5 times as long as carpus.

Abdomen smooth; fifth abdominal segment with pleura ending in an acute tooth, sometimes extremely small; sixth segment half again as long as fifth, somewhat shorter than telson. Telson with two pairs of dorsal spines; anterior pair somewhat behind middle; second pair halfway between these and tip; posterior margin with strong median point flanked by two pairs of spines, inner pair longest, and between them two feathered setae. Outer margin of uropodal exopod with a strong terminal tooth flanked by a slender movable spine medially.

Measurements.—Length of body: male, 33 mm.; ovigerous females, 30 to 50 mm.

Variations.—Males differ from females as follows: smaller size, more slender rostrum, free part of shorter ramus of upper antennular flagellum longer in relation to fused part, somewhat shorter legs, and carpus of second leg longer in relation to chela. Young individuals resemble males (Holthuis, 1952). The second chelae of a few females have one small tooth on the cutting edge of the dactyl.

Color.—Transparent in life.

Habitat.—Estuarine waters, especially in beds of submerged vegetation.

Type locality.—Lagoon near Cove Point Light, Chesapeake Bay.

Known range.—Essex County, Mass., to Port Aransas, Tex. (from specimens examined by Holthuis, 1952). Literature records: Cold Spring Harbor, Long Island, N.Y., to Corpus Christi, Tex.

Remarks.—The confused taxonomic status of this species in literature is discussed in the account for *P. vulgaris* and dealt with in more detail by Holthuis (1952).

Broad (1957a) worked out the larval development of *P. pugio* and *P. vulgaris*. He found mature individuals of both species were abundant in the Beaufort, N.C., area from April until mid-

October. Larval development of the 2 species is similar, and 10 zoeal stages and a postlarval stage were described for both. The chief difference between larvae of the two species is in the presence of a pair of chromatophores found on the second abdominal sternite of *P. pugio* but lacking in *P. vulgaris*. The number of larval stages and length of the developmental period may vary, and such variation is apparently due to availability of suitable food. In rearing *Palaeomonetes* with artificial diets, Broad (1957b) found that algae alone were not sufficient to promote survival; mixtures of plant and animal food were better, but best survival was obtained by feeding living *Artemia* nauplii. Frequency of molting and rate of development were directly correlated with amount of suitable food available.

Responses of the white chromatophores of *P. pugio* to light and temperature have been investigated by Fingerman and Tinkle (1956). The tendency of white pigment to disperse in bright light, especially on a white background, is normally antagonized by a tendency of the pigment to concentrate with increased temperature. This mechanism is interpreted as maintaining a steady state of white chromatophores in nature.

Pearse (1952b) reported *Probopyrus pandicola* (Parkard) from the gill chamber of this species in Texas.

Family Gnathophyllidae

Caridea with first two pairs of legs chelate, first pair smaller than second; carpus of second pair not subdivided. Rostrum short and toothed. Third article of third maxillipeds very broad. Mandibles simple. Second maxillipeds with short seventh article. The family contains but a single genus (Hay and Shore, 1918).

Genus *Gnathophyllum* Latreille, 1819

Armstrong, 1940, p. 6 (rev.).—Hemming, 1958b, p. 156.

Gnathophyllum modestum Hay

Figure 50

Gnathophyllum modestum Hay, 1917, p. 72.—Hay and Shore, 1918, p. 395, pl. 28, fig. 1.—Manning, 1963, p. 48, figs. 1-2.

Recognition characters.—Body short and thick; carapace with a moderate carina continuous in front with rostrum and extending about two-thirds of distance to posterior margin. Rostrum

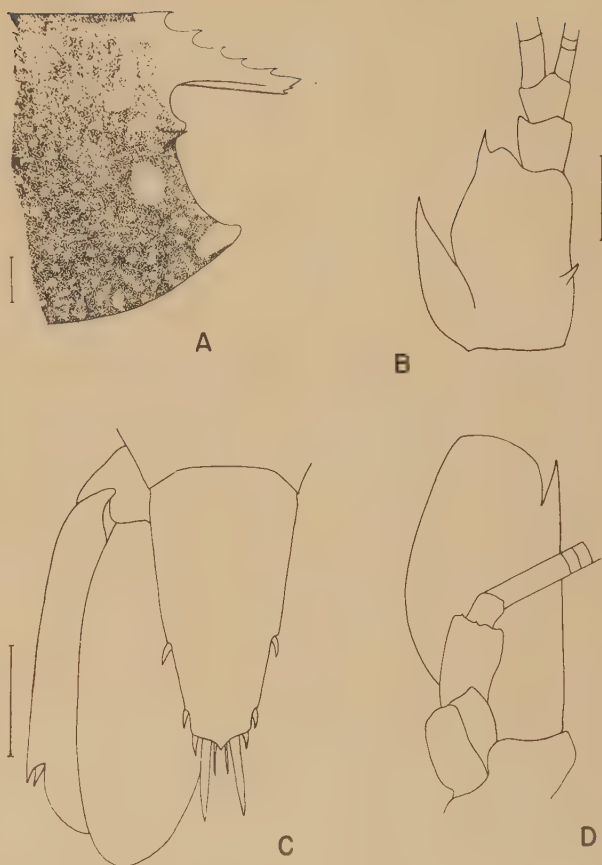


FIGURE 50.—*Gnathophyllum modestum* Hay. A, anterior portion of carapace, lateral view; B, antennular peduncle, ventral view; C, telson and left uropod; D, antennal scale; 1 mm. indicated, B and D to same scale (after Manning, 1963).

obliquely truncate dorsally and armed with five or six dorsal teeth; one or two small ventral teeth near tip; tip reaching to distal end of basal article of antennule. Suborbital angle prominent; antennal spine present; anterolateral angle strongly produced. Eyes rather large and with a prominent, conical, black protuberance on cornea. Antennular peduncles with basal article large, stylocerite reaching beyond middle of article, a spine at anterolateral corner of article; second article with a similar but smaller and blunter anterolateral spine; second and third articles of about equal length; outer antennular flagellum bifurcate, upper ramus longer and thinner than lower ramus. Antennal scale reaching beyond antennular peduncles, lateral margin almost

straight, terminating in a spine, lamella of scale rounded distally, slightly exceeding spine.

Third maxillipeds with merus and carpus broad, closing whole front of buccal region; two terminal articles flattened, much more slender, and extended straight forward. Second pair of legs much stronger than first, exceeding rostrum by length of chela; fingers more than half length of palm. Last three pairs of legs with dactyls bifurcate.

Abdomen with last three segments abruptly smaller than preceding segments and strongly flexed. Telson with a pair of marginal spines at about distal third and a minute pair near tip, tip with median point and with three pairs of spines, intermediate pair longest.

Measurements.—Length of ovigerous holotypic female, 21 mm.

Color.—Body deep brown with many scattered small yellow and a few larger orange spots; antennal scale, distal portions of rostrum and tail fan clear; orbital margins and eyestalks white; legs grading from brown proximally through purple to white distally but barred with purple on distal portion of some elements; markings of yellow below and on some articles of appendages (Manning, 1963).

Habitat.—Found around clumps of coral and sponges in shallow water; to 15 fathoms.

Type locality.—Beaufort, N.C.

Known range.—Beaufort, N.C.; Biscayne Bay, Fla.

Remarks.—This species, long known only from Hay's type specimen, has recently been reported from Florida (Manning, 1963). Manning reviewed the east American species of *Gnathophyllum*, pointing out the close similarity of *G. modestum* to the eastern Atlantic species *G. elegans*, and giving detail on the importance of color patterns in living material as diagnostic characters in the genus. Excellent figures accompany Manning's discussion.

Ovigerous females are known from Florida in June. The date of collection for Hay's specimen is unknown.

Family Alpheidae

Carapace smooth, with cardiac grooves; rostrum reduced; antennal and branchiostegal spines always absent; carapace almost always projecting

over eyes (*Automate* excepted). Antennular base cylindrical, basal article not longer than sum of other two articles. Antennal scale rarely longer than antennal peduncle. Mandible bipartite with palp of two points. Chela of first leg predominant, always large (usually asymmetrical); carpus short. Second legs weakly developed; carpus multiarticulate. Third to fifth legs with spinous propodi and simple or bifurcate dactyls; propodus of fifth leg with more or less well-developed brush of bristles in transverse to oblique rows. Abdomen usually with gradual curve, no pronounced bend at third segment; sixth segment short, broad, sexually dimorphic. (Adapted from Banner, 1953).

The biology of snapping shrimp occurring on the east coast of the United States has been reviewed by Knowlton (1960) and the reader is referred to this unpublished but useful work for more complete information than is included here.

KEY TO GENERA IN THE CAROLINAS

- a. Eyestalks completely exposed
Automate kingsleyi (p. 62).
- aa. Eyestalks covered by carapace.
 - b. Epipods present on at least first two pairs of legs
Alpheus (p. 63).
 - bb. Legs without epipods.....*Synalpheus* (p. 69).

Genus *Automate* de Man, 1887

Man, J. G. de, 1887, p. 529.

Automate kingsleyi Hay

Figure 51

Automate kingsleyi Hay, 1917, p. 72.—Hay and Shore, 1918, p. 387, text-fig. 10; pl. 26, fig. 7.

Recognition characters.—Carapace about half length of abdomen; subcylindrical; deeply emarginate dorsally behind eyestalks with rostrum a small median projection; anterior margin entire, produced farthest forward at base of antennular and antennal peduncles. Eyestalks contiguous, broad at base; cornea well developed with a minute point on anterior surface in lateral view. Antennular and antennal peduncles long; stylocerite scalelike, reaching to end of basal antennular article; second antennular article nearly equal in length to first; third very short. Antennal scale extending to middle of terminal article of antennal peduncle; lateral border ending in a small spine; lamella broadly rounded distally, equaling spine. Third maxilliped exceeding an-

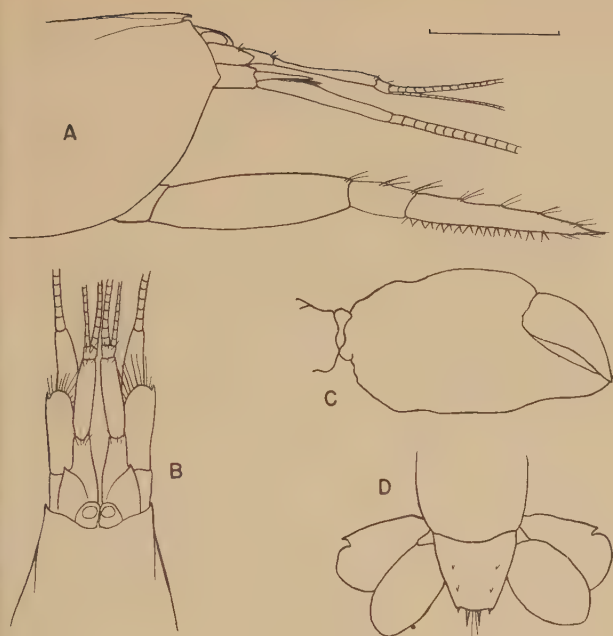


FIGURE 51.—*Automate kingsleyi* Hay. A, anterior part of ovigerous female in lateral view; B, anterior part of body in dorsal view; C, large chela; D, uropods and telson in dorsal view; 1 mm. indicated (C after Hay and Shore, 1918).

tenna peduncle by less than length of terminal article.

First pair of legs chelate, prismatic, unequal; larger one appearing somewhat rougher and stouter than smaller one; fingers slightly gaping, immovable finger in line with hand and broad at base; dactyl narrower and moderately curved; carpus short; merus nearly as long as dactyl. Second pair of legs nearly as long as first but slender, weakly chelate, and with carpus divided into five joints with proportions of 1 : 1.25 : 0.80 : 0.66 : 0.80. Third to fifth legs with dactyls simple.

Abdomen well developed; compressed; with strong pleopods. Telson tapering; truncate terminally, ending in two short lateral spines flanked medially by two longer spines and a median pair of feathered setae; dorsally armed with two pairs of spines, first pair at midlength, second at three-fourths length. Uropods with oval blades; lateral border of exopod deeply notched distally, border ending in a small tooth flanked medially by a strong movable spine.

Measurements.—Length of body: ovigerous females, 7 to 16 mm.

Color.—Almost transparent except for a small amount of red pigment on appendages and telson.

Habitat.—Unknown.

Type locality.—Shark Shoal breakwater, near Beaufort Inlet, N.C.

Known range.—Known only from and near type locality, and from Pelican Island, English Harbor, Barbados (Schmitt, 1924a).

Remarks.—Aside from the Barbados specimen, only three specimens from the Beaufort, N.C., area are known. The ovigerous type was taken July 9, 1916, and another ovigerous female on September 7, 1960. The third specimen is immature. Hay and Shore (1918) reported that the type remained alive in the laboratory for over a month, during which time the eggs dropped off and the specimen molted twice without appreciably increasing in size.

Genus *Alpheus* Fabricius, 1798

Banner, 1953, p. 46.—Hemming, 1958b, p. 108.

The status of the name *Alpheus* (and its confusion in usage with the name *Crangon*, at least among American workers during the first half of this century) was in doubt until nomenclatural stability was effected by the International Commission on Zoological Nomenclature (Opinion 334). The Official List of Generic Names in Zoology (Hemming, 1958b) now lists *Alpheus* Fabricius, 1798, as the correct generic name for the species here considered, and the Official Index of Rejected and Invalid Generic Names in Zoology (Hemming, 1958a) lists the suppressed generic names *Alpheus* Weber, 1795, and *Crangon* Weber, 1795, formerly applied to the species here considered.

KEY TO SPECIES IN THE CAROLINAS

- a. Orbital hoods of carapace with a small spine in front
formosus (p. 64).
- aa. Orbital hoods of carapace without a distinct spine.
 - b. Orbital hoods forming an anterior toothlike projection; large hand with a groove above and below along outer margin and between these grooves a thick tooth
normanni (p. 65).
 - bb. Orbital hoods rounded anteriorly; large hand broad and notched on both margins.
 - c. Base of rostrum passing gradually into lateral dorsal surface.....*heterochaelis* (p. 66).
 - cc. Base of rostrum with borders sharply defined
armillatus (p. 67).

Alpheus formosus Gibbes. Striped snapping shrimp

Figure 52

Alpheus formosus Gibbes, 1850, p. 196.—Verrill, 1922, p. 84, text-figs. 5d, 6a; pl. 20, fig. 3; pl. 23, figs. 5 a, b; pl. 29, figs. 4, a-u; pl. 25, figs. 6-6a.

Crangon formosus: Hay and Shore, 1918, p. 384, pl. 26, fig. 5.—Schmitt, 1935a, p. 144.

Recognition characters.—Rostrum beginning at posterior line of eyes and reaching about to second article of antennular peduncle; flat above; margins concave at base but regularly convergent anteriorly and with scattered stiff hairs; tip rounded, often bearing two or three minute spines. Carapace half length of abdomen, compressed, not grooved; orbital hoods each with an acute, anteriorly directed spine much shorter than rostrum; anterior margin emarginate below orbital hoods. Eyes completely covered by carapace. Antennular peduncles with scalelike stylocerite, slender tip reaching slightly beyond basal article; second article twice length of third; inner flagellum filiform, outer flagellum thick proximally, filiform distally. Antenna longer than body;

antennal scale with strong apical spine reaching to or beyond tip of antennular peduncle, spine separated from and exceeding lamella; a weak spine (basicerite) below near base of scale. Third maxillipeds with terminal joint hairy; slightly exceeding antennal peduncle.

First legs strongly chelate, very unequal. Larger leg compressed, smooth above and unnotched along margins; immovable finger acute, incurved at tip, shorter than stout and gradually arched, blunt dactyl; carpus short, convex above, with a distal tooth; merus with an acute distal spine. Smaller chela much more slender, long, and smooth, inner surface with a stout spine overhanging base of dactyl; immovable finger nearly straight, slender, somewhat turned up near tip; dactyl about half length of hand, nearly straight to about middle, then gently arched to tip, hairs arising from a nearly straight groove below ridge on both sides; inner surfaces of fingers with a slender groove and carina; fingers shutting closely. Second pair of legs slender; weakly chelate; carpus subdivided, with joints diminishing in length as follows (numbered from proximal end): 1, 5, 2, 3-4. Third to fifth legs with simple dactyls.

Telson with two pairs of dorsal spines at about one-third and two-thirds length; posterolateral corners with a pair of spines, medial spine much longer than lateral, distal margin with long hairs. Uropodal exopods with lateral margin ending in a black movable spine between two fixed spines; black spine remaining amber colored after long preservation.

Measurements.—Length of body: ovigerous females, 17 to 35 mm.

Color.—Color pattern conspicuous and characteristic; ground color yellowish or greenish brown finely speckled with orange; a narrow light stripe along middorsal line extending from distal end of antennular peduncle to base of telson, line light orange anteriorly merging into yellowish green and finally gray posteriorly, a brown stripe on each side dorsolaterally and below this another stripe of white, or colors similar to dorsal stripe, along each side followed by a stripe of light reddish brown and still another stripe of blue-bordering abdomen; chelae greenish brown with orange red fingers; antennules, antennae, and walking

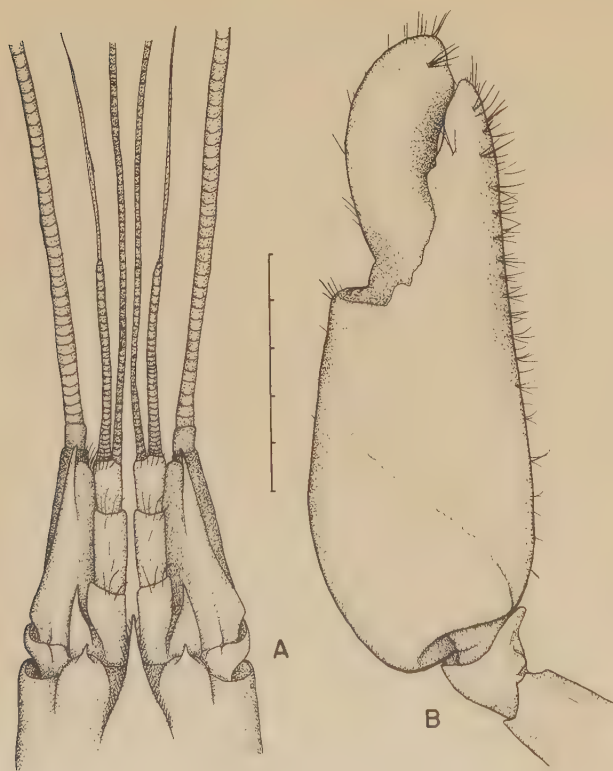


FIGURE 52.—*Alpheus formosus* Gibbes. A, anterior part of body in dorsal view; B, outer surface of large chela; 5 mm. indicated.

legs blue; telson and uropods white at base blotched and bordered with yellow.

Habitat.—Lives in holes and crevices in shell bars, stones, and dead corals; water's edge to 23 fathoms.

Type locality.—Key West, Fla.

Known range.—Near Beaufort, N.C., through West Indies to Santos, São Paulo, Brazil; Bermuda.

Remarks.—Ovigerous females have been taken off Venezuela in April, Beaufort, N.C., in July, Bimini in October, and Santos, Brazil, in June. Manter (1934) found metacercariae of *Helicometrina nimia* encysted in muscles of *A. formosus* at Tortugas.

Alpheus normanni Kingsley. Green snapping shrimp

Figure 53

Alpheus affinis Kingsley, 1878a, p. 195.

Alpheus normanni Kingsley, 1878b, p. 93.

Alpheus packardii Kingsley, 1880, p. 417.—Verrill, 1922, p. 80, pl. 20, figs. 2-5; pl. 21, fig. 5; pl. 22, fig. 7; pl. 23, figs. 6, c-d; pl. 25, figs. 4, a, b; pl. 31, figs. 1, b-1, 2, b-u, 3, u, t (rev.).

Orangon packardii: Hay and Shore, 1918, p. 385, pl. 26, fig. 4.—Schmitt, 1935a, p. 144.

Recognition characters.—Rostrum with carina extending as far back as base of eyestalks, spiniform tip not reaching to base of second article of antennule. Carapace about two-thirds length of abdomen, somewhat compressed; cervical groove hardly evident; front with ocular hoods produced into an obtuse angle above each eye; anterior margin emarginate below ocular hoods. Eyes well developed but completely covered by carapace. Stylocerite scalelike with spiniform tip reaching about to end of basal article of antennule; third article much shorter than second; inner antennular flagellum slender, outer one shorter with proximal four-fifths enlarged. Antennae a little longer than body, slender; antennal scale reaching a little beyond end of antennular peduncle, lateral margin slightly sinuous with strong terminal spine separated from and exceeding lamella; a strong ventral spine (basicerite) near base of scale. Third maxillipeds slender, not reaching tip of antennal scale; terminal article with long hairs.

First legs strongly developed with chelae unequal. Larger leg broad and flattened; slightly sinuate along inner margin; outer margin with a longitudinal groove above and below, a ridge

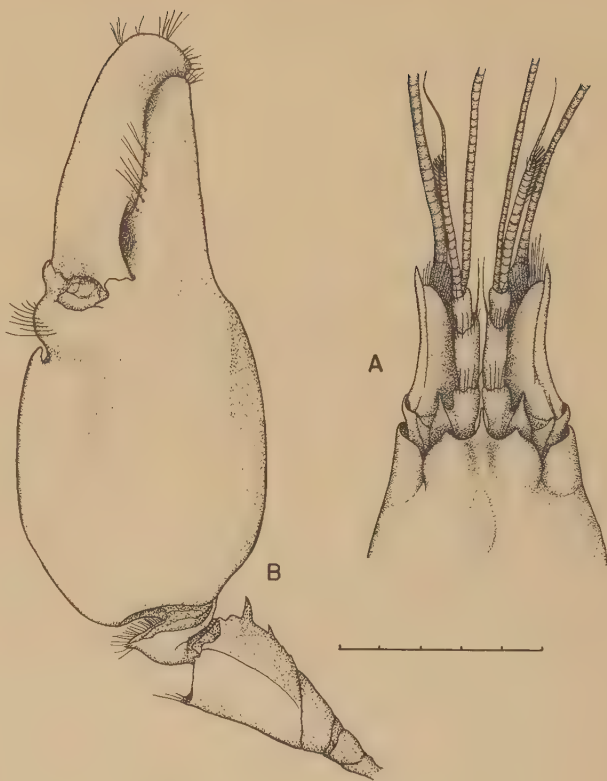


FIGURE 53.—*Alpheus normanni* Kingsley. A, anterior portion of body in dorsal view; B, large chela in ventrolateral view; 5 mm. indicated.

between grooves ending in a strong tooth behind base of dactyl; dactyl heavy, curved, toothed at base. Smaller chela about half as wide and three-fourths as long as larger one; similarly formed but with a sharp spine above (and a small one below in males) at base of dactyl; no basal tooth on dactyl; sexually dimorphic fingers in males broad externally but with keeled, closely fitting opposed edges fringed by dense hairs; females with hand a bit hairy but fingers unornamented; carpus of both legs short, broad, irregularly cup shaped, merus with a spiniform tooth near distal end and one or two spines below, distal end cupped to receive carpus with leg extended. Second legs very slender, weakly chelate; with carpus subdivided, joints diminishing in length as follows (numbered from proximal end): 2, 1, 5, 3-4. Third to fifth legs with dactyls simple.

Abdomen somewhat compressed. Telson with sides slightly convergent distally; two pairs of dorsal spines, first pair at one-third, second at

two-thirds length; tip broadly rounded, a pair of spines at each posterolateral corner, distal margin heavily setose; a pair of anal tubercles beneath with accompanying cups on uropods forming locking devices. Uropods oval; exopod with lateral margin ending in a small spine flanked medially by a strong movable tooth.

Measurements.—Length of body: male, 26 mm.; ovigerous female, 16 mm.

Color.—Gray or dull green, sometimes with a median and lateral stripe of whitish often clouded or mottled with dark green or brown, a paler spot behind each eye; large chela dark green usually banded with yellowish brown or yellow on inner surface; smaller chela and other legs paler, often banded with dull gray or reddish; occasionally body banded with red and pale yellow, large chela with two pale bands, immovable finger blackish, dactyl reddish (various authors).

Habitat.—Shelly or rocky bottoms, in burrows in sand or on pilings in shallow water; common in saltier portions of estuaries; water's edge to 40 fathoms.

Type locality.—Key West, Fla.

Known range.—North Carolina through West Indies to Barbados, Curaçao, and Aruba; Alligator Harbor, Fla., to Sabine, Tex.; Bermuda; Sonora, Mexico(?).

Remarks.—This is one of the commonest snapping shrimps in the Beaufort, N.C., region. As Hay and Shore (1918) pointed out, this was probably the species called *Alpheus minor* in early lists for the area. The latter species is correctly referred to *Synalpheus minus* (Say) and is found only in offshore waters, a different habitat from that frequented by *Alpheus normanni*. Brooks and Herrick (1892) followed the older lists in calling this species *Alpheus minor* (*minus*) and illustrated the adult in color on plate 1 and larval stages on plates 16 and 17. They illustrated the first three larval stages, as well as stages in segmentation of the embryo, but their specific identifications are somewhat unreliable.

Ovigerous females have been taken through much of the annual cycle in various localities: January and March, Cuba; June, Louisiana; August, Bermuda, Louisiana, Mississippi; April to September in the Carolinas; November and December, Puerto Rico.

Alpheus heterochaelis Say. Big-clawed snapping shrimp

Figure 54

Alpheus heterochaelis Say, 1818, p. 243.—Verrill, 1922, p. 76, pl. 22, figs. 1, 2, 4, a-c; pl. 24, figs. 7, 7a; pl. 30, figs. 1-1a, 1t, 2a-2e; pl. 33, figs. 1, 2 (rev.).

Crangon heterochaelis: Hay and Shore, 1918, p. 386, text-fig. 8, pl. 26, fig. 6.—Schmitt, 1935a, p. 144.

Recognition characters.—Rostrum carinate, extending back about as far as base of eyestalks; tip not reaching to base of second article of antennular peduncle. Carapace more than half length of abdomen, somewhat compressed; without grooves; front produced into a rounded ocular hood over each eye; rostro-orbital depressions passing gradually into dorsal surface; emarginate below eye on anterior border. Eyes relatively small, covered by carapace. Antennular peduncles with scalelike stylocerite, minute spine at tip not reaching end of basal article; second article twice length of third; inner flagellum filiform, about half length of antenna; outer flagellum with proximal two-thirds thickened. Antennae a little longer than body; antennal scale with strong apical spine reaching slightly beyond antennular

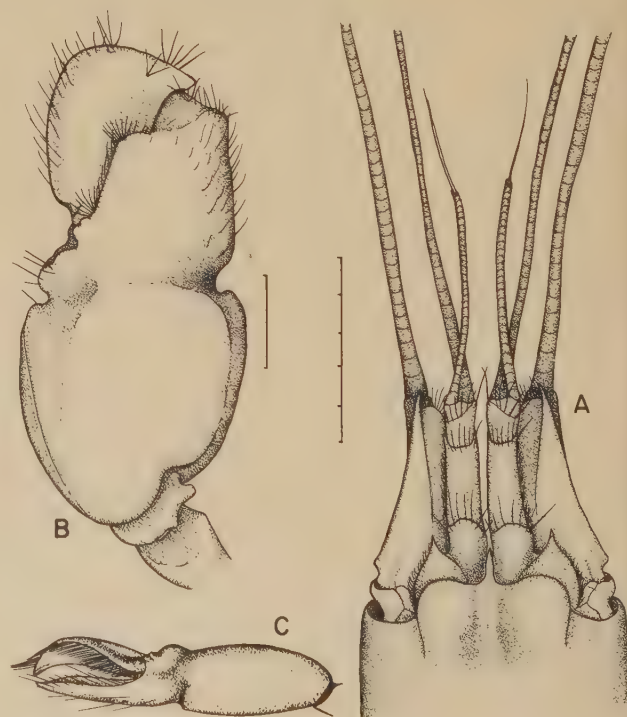


FIGURE 54.—*Alpheus heterochaelis* Say. A, anterior portion of body in dorsal view, 5 mm. indicated; B, large chela in dorsal view, 5 mm. indicated; C, small chela of male (after Verrill, 1922).

peduncle, spine separated from and slightly exceeding lamella; a weak spine (basicerite) below near base of scale. Third maxillipeds with terminal article hairy; slightly exceeding antennal peduncle.

First legs strongly chelate, very unequal. Larger chela thick; outer and inner margins deeply notched near base of fingers; upper and lower surfaces with irregular shallow grooves; dactyl broad, heavy, strongly curved, with large basal tooth. Small chela sexually dimorphic; in male broad, elongate; proximal dorsal area of palm bounded by an impressed line, upper margin notched distally; dactyl flattened and expanded on outer surface; opposed edges of fingers keeled, closely fitting, fringed by dense hairs. Fingers of small chela in both sexes weaker, less curved, and more hairy than in large chela; carpus short; merus smooth. Second legs slender, weakly chelate; carpus subdivided with joints diminishing in length as follows (numbered from proximal end): 1, 2, 5, 4, 3. Third to fifth legs with simple dactyls.

Abdomen compressed, smooth, tapering. Telson with subparallel sides and rounded tip; dorsal surface with two pairs of movable spines, first pair at about midlength, second at a little less than three-fourths length; a pair of spines at each posterolateral corner, medial spine longest; distal margin heavily setose, a pair of anal tubercles beneath with accompanying cups on uropods forming locking devices. Uropodal exopods with lateral border ending in a fixed spine flanked medially by a longer movable spine.

Measurements.—Length of body: male, 40 mm.; female, 50 mm.

Color.—Dark translucent green, slightly flushed with purple on sides of carapace; white markings on chelipeds; walking legs pale red; tips of uropods blue with narrow border of orange on distal margin, outer blade with patch of red just above blue, and a narrow white border; articular surfaces and joints of abdominal segments, and a small streak along cervical groove, white.

Habitat.—Lives among broken shells and stones or in burrows in mud among shells; water's edge to 16 fathoms.

Type locality.—Amelia Island, Nassau County, Fla. (Holthuis, 1959, restr.).

Known range.—Near Hatteras, N.C., to Aransas County, Tex.; Colon, Panama; through West Indies to Iguape, São Paulo, Brazil; Bermuda (Holthuis, 1956).

Remarks.—Brooks and Herrick (1892) gave a good colored figure of this species (plate 2), as well as a series of figures of segmenting eggs and developing larval stages. Because the material they studied originated from both North Carolina and the Bahamas, there is some doubt as to its identity, but a total of four larval stages were illustrated.

This is the largest snapping shrimp found in the Carolinas. It is nearly as abundant as *A. normanni*.

Ovigerous females have been taken through much of the annual cycle in various localities: February and April in Surinam (Holthuis, 1959); March in Panama and Texas; April and May in Louisiana and Florida; July in North Carolina; August and September on the Gulf Coast; October to January in Cuba, Puerto Rico, and Bonaire.

Alpheus armillatus Milne Edwards. Banded snapping shrimp

Figure 55

Alpheus armillatus H. Milne Edwards, 1837, p. 354.—Verrill, 1922, p. 73, text-figs. 5a, 6b; pl. 20, fig. 4b; pl. 21, figs. 4, 4a; pl. 26, figs. 1-1d; pl. 23, fig. 4; pl. 27, figs. 1-1s (rev.).

Crangon armillatus: Hay and Shore, 1918, p. 386, text-fig. 9; pl. 27, fig. 1. Schmitt 1935a, p. 142.

Recognition characters.—Rostrum in form of a narrow raised crest from base to tip, projecting beyond orbital hoods, widening abruptly just behind eyes into a triangular area with borders slightly concave and distinctly limiting rostro-orbital depressions, slightly overhanging depressions in adult specimens. Carapace compressed; orbital hoods prominent in front with a slight obtuse anterior lobe, but without spine or denticle, and with a strong emargination below eyes. Eyes entirely covered by carapace. Antennules with stylocerite large, scalelike, not very acute, and not reaching to end of basal antennular article; second article longer than third; inner flagellum filiform; outer flagellum thickened in about proximal half. Antennal scale with a strong terminal spine equal to or extending beyond antennal peduncle, scale distinctly curved outward in distal two-thirds; a small spine (basicerite) near base of scale. Third

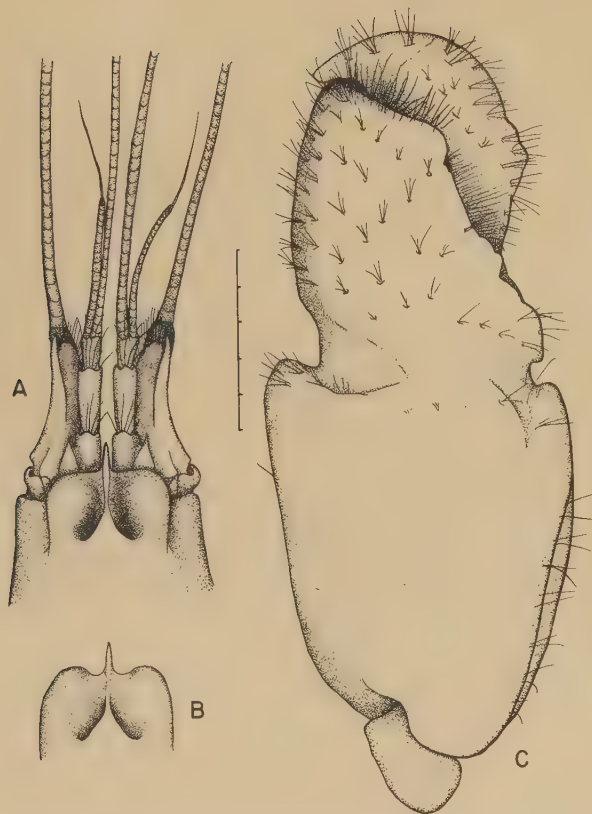


FIGURE 55.—*Alpheus armillatus* Milne Edwards. A, anterior portion of body in dorsal view; B, rostral region in dorsal view with light showing from posterior; C, large chela in dorsal view; A–C, 5 mm. indicated.

maxilliped covered with long hairs distally, reaching about to end of antennal peduncle.

First legs strongly chelate, hairy, unequal. Larger chela thick; outer and inner margin deeply notched near base of fingers; upper and lower surfaces with irregular shallow grooves; dactyl broad, heavy, curved, with large basal tooth. Small chela slender; cutting edges of fingers closely fitting, dactyl with a small tooth at base, dactyl in males lacking setose crests and expanded external surface characteristic of *A. heterochaelis*. Second legs long, slender, weakly chelate, with part of merus reaching beyond rostrum; carpus subdivided with joints diminishing in length as follows (numbered from proximal end): 1, 2, 5, 3–4. Third to fifth legs with simple dactyls.

Abdomen smooth, compressed. Telson with two pairs of dorsal spines, first pair at one-third, second at two-thirds length; sides somewhat

convergent distally, tip rounded, with a pair of spines at each posterolateral corner, medial spine twice length of outer spine. Uropodal exopod with outer margin ending in a small spine flanked medially by a larger spine.

Measurements.—Length of body: ovigerous females, 31 to 38 mm.

Color.—Body with dark gray or brown ground color, crossed by nine conspicuous lunate or elliptical spots or bands of translucent white equal in width to intervening dark bands; carapace with three white bands, third one at posterior margin; abdomen with six bands, first blending with last on carapace; abdominal bands usually whiter or more clearly defined than bands on carapace; abdomen often dark green with spots bordered by line of orange; uropods and telson usually with a broad crossband and sometimes tipped with orange; chelae thickly speckled with dark gray, whitish bands above, tipped with pale pink or white; antennal peduncles grayish, flagella and walking legs orange yellow banded with white (Verrill, 1922).

Habitat.—Under rocks and shells or in holes in rocks; shallow water.

Type locality.—West Indies.

Known range.—North Carolina, through West Indies to Cananéia, São Paulo, Brazil; Bermuda (Holthuis, 1956).

Remarks.—This species closely resembles *A. heterochaelis*, its similar sized and (in the Carolinas) much more abundant congener. *Alpheus armillatus* is named for its conspicuously banded body, but in preserved material it can be distinguished from similar species by the distinctive form of the rostrum and from *A. heterochaelis* males by the lack of the specialized dactyl on the small first chela.

The species is rarely taken in the Beaufort region of North Carolina. Hay and Shore (1918) found males and females living in pairs under rocks at Fort Macon. Ovigerous females are known from only the first half of the annual cycle: March, Panama; April, Venezuela; May, Barbados; June, Florida and Brazil; August, Bermuda.

Pearse (1932b) reported encysted larvae of *Rhyncobothrius* in viscera of *A. armillatus*.

Coonfield (1940) observed the chromatophore system of this shrimp in one of the early studies

of this kind, showing that it reacts to different backgrounds under varying light conditions.

Hess (1940, 1941) demonstrated that *A. armillatus* is sensitive to light in many regions of the body, regardless of the amount of time elapsed since the preceding molt. At Tortugas, he found that diurnal molting in this shrimp is apparently controlled by daily temperature changes, molting occurring when the temperature rises to or above 29° C. Animals in constant temperature failed to exhibit diurnal molting as did ovigerous females.

Darby (1934) studied regeneration of chelae in *A. armillatus* and *Synalpheus longicarpus* together with determination of right or left handedness. He found that in development of chelae a stage was reached that permitted determination of which side would have a large chela. Equal chelae were produced experimentally and were of three varieties: (1) both small (pinch claws); (2) both large (snap claws); and (3) both intermediate.

Darby offered an hypothesis, involving two substances and a metabolic condition, which could explain the regenerative phenomena in these and allied crustaceans. In such animals, a substance A is produced which controls production of pinch claws; but at certain stages in the intermolt cycle a substance B is produced, for a limited time, and is concentrated in whichever claw is regenerating or already modified as a snap claw. This circumstance will produce or reinforce production of a snap claw. Chance alone is responsible for whether a snap claw will be on one side or the other, or whether the animal will be symmetrical. Also, time at which regeneration occurs depends on chance.

Genus *Synalpheus* Bate, 1888

Banner, 1953, p. 26.—Hemming, 1958b, p. 161.

KEY TO SPECIES IN THE CAROLINAS

- a. Dactyls of third, fourth, and fifth legs with two very unequal hooks, ventral strongest (broadest); an inconspicuous, obtuse supernumerary process proximal to ventral hook.....*fritzmuelleri* subsp. (p. 69).
- aa. Dactyls of third to fifth legs with two hooks approximately equal in width at base.
 - b. Dactyls long and slender, hooks continuing general direction of axis of dactyl; stylocerite longer than basal article of antennular peduncle; lamella of antennal scale present.

c. Frontal teeth more or less equilaterally triangular, at times with concave margins, but never with an inferior vertical prolongation to rostrum; basicerite strongly spinous above

minus (p. 70).

cc. Frontal teeth always longer than wide, spinous; rostrum armed with a ventral prolongation which embraces ocellary beak; basicerite unarmed above.....*townsendi* (p. 72).

bb. Dactyls short, hooks strongly curved, ventral one usually bent at considerable angle to axis of dactyl; stylocerite not exceeding first article of antennular peduncle; antennal scale lacking lamella in male, small in female.....*longicarpus* (p. 73).

Synalpheus fritzmuelleri Coutiere

Figure 56

Synalpheus fritzmuelleri Coutiere, 1909, p. 35, fig. 18.—Ver-rill, 1922, p. 97. Schmitt, 1935a, p. 148.

Recognition characters.—Rostrum slender, compressed, acute from dorsal view, a little longer than orbital spines, reaching to midlength of visible portion of basal antennular article. Orbital spines wide at base, acuminate; margins incurved. Eyes completely covered by carapace. Antennular peduncle with stylocerite of basal article reaching

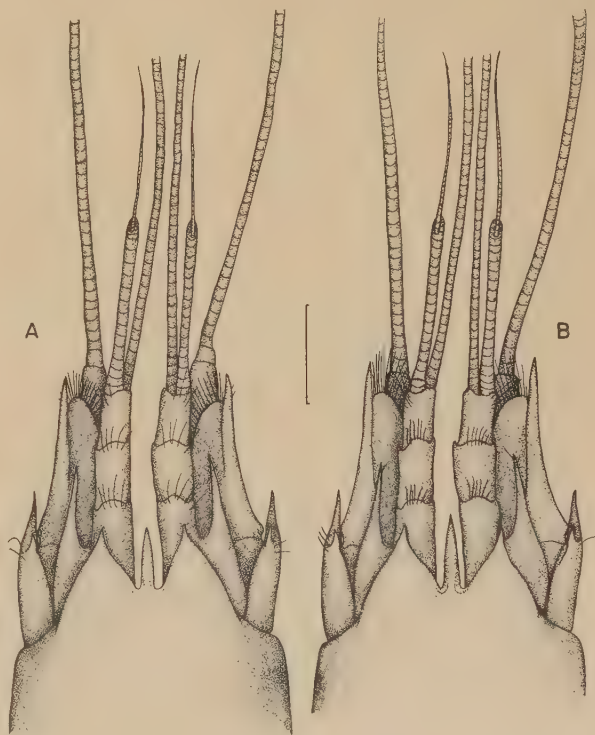


FIGURE 56.—A, *Synalpheus fritzmuelleri* Coutiere, anterior portion of animal in dorsal view; B, *Synalpheus fritzmuelleri elongatus* Coutiere, anterior portion of animal in dorsal view; 1 mm. indicated.

to middle of second article; third article slightly shorter than second; inner flagellum filiform outer bifurcate beyond about eighth joint, thickened proximally. Spine of antennal scale equaling terminal article of antennal peduncle, both reaching a little beyond antennular peduncle, spine separated from and exceeding narrow lamella distally; basicerite with a short, sharp lateral spine nearly as long as stylocerite; above it a smaller, acute, secondary spine.

First pair of legs chelate, unequal. Large chela ellipsoidal, only a little swollen in middle; a small obtuse tubercle on distal dorsal margin; width of palm about one-third total length of chela; dactyl heavy, strongly arched above; immovable finger narrow at tip; carpus short and wide, prolonged downward and inward; merus stout, superior margin ending distally in a sharp angular point. Smaller chela similar in form; fingers pointed; carpus short, cup shaped; merus like that of larger chela. Second legs slender, weakly chelate; carpus subdivided, first joint about equal to remaining four. Third to fifth legs with bifurcate dactyls, hooks unequal; outer one thinner and a little longer, regularly curved, sharp; inner one wider at base, strongly divergent, curved inward; proximal to inner hook a slight obtuse protuberance or rudimentary spur.

Telson broad, tapering, obtusely rounded distally; each posterior angle with a pair of unequal spines; two pairs of small dorsal spines, first pair at midlength, second at three-fourths length. Uropodal exopods with lateral margin ending in a notch with a fixed spine on each side, a longer movable spine between them.

Measurements.—Length of body: ovigerous female, 22 mm.

Variations.—In the subspecies *S. f. elongatus* Coutiere (1909, p. 37, fig. 19) the lateral spine of the antennal scale greatly exceeds the terminal article of the antennal peduncle, and the rostrum is decidedly longer than the ocular spines. In the subspecies *S. f. carolinensis* Verrill (1922, p. 99, pl. 22, fig. 6; pl. 39, figs. 1-1d) and *S. f. caribaea* Verrill (1922, p. 98, text-fig. 8; pl. 39, figs. 3a-3c) the basicerite is shorter than in typical specimens.

Color.—*Synalpheus fritzmuelleri*: chela varying shades of green, darker toward extremities of fingers; body more or less colorless, speckled with

quite numerous tiny red chromatophores. *Synalpheus fritzmuelleri elongatus*: similar to preceding; chelipeds and second legs blue, except anterior part of chela light green (Schmitt, 1930).

Habitat.—Often found living in sponges; low tide mark to 28 fathoms.

Type locality.—*Synalpheus fritzmuelleri*, Marco, Fla.; *S. f. elongatus*, Mouth of Bull Creek, S.C.

Known range.—Typical *fritzmuelleri*: Nege, Greenland (Stephensen, 1950); off Beaufort, N.C., to Port Aransas, Tex.; West Indies to Curaçao; Old Providence Island; Tres Marias Archipelago, Mexico; Bermuda. Subspecies *elongatus*: off Beaufort, N.C., to Florianopolis, Santa Catarina, Brazil, including Jamaica and Barbados; Tres Marias Archipelago, Mexico. Subspecies *carolinensis*: Fort Macon, N.C. Subspecies *caribaea*: Dominica.

Remarks.—Distribution of the named subspecies and varieties of *Synalpheus fritzmuelleri* shows that modern revisionary work in the Western Atlantic is needed. Until thorough study is made, the various names must be retained, but it is likely that the present designations do not adequately explain local populations which parallel each other at widely separated locations. As Banner (1953) pointed out, earlier workers, with only a few specimens from these widely separated localities, naturally tended to name the variants, the range of variation being then unknown. Varietal names, therefore, must be regarded as conditional. Verrill (1922, p. 89) may have concurred for he quoted Stebbing's dim view of naming infinite variations but proceeded to name varieties anyway.

In the Carolinas, this species lives on offshore reefs (Pearse and Williams, 1951) in large sponges. Specimens may be found in beach drift after severe storms. Ovigerous females of typical *fritzmuelleri* are known from the Carolinas in February, and June to October, indicating a long breeding season. Ovigerous females of *S. f. elongatus* are known from Barbados in May, and North Carolina in June and July.

Synalpheus minus (Say)

Figure 57

Alpheus minus Say, 1818, p. 245.

Synalpheus minus: Hay and Shore, 1918, p. 382, text-fig. 5; pl. 26, fig. 3 (rev.).—Verrill, 1922, p. 102, pl. 21, fig. 1; pl. 23, fig. 3; pl. 25, fig. 3; pl. 31, fig. 4; pl. 33, figs. 4, 4a; pl. 36, figs. 1-1d, 2; pl. 47, figs. 1-1c, 2; pl. 48, figs. 3-3c (rev.).—Schmitt, 1935a, p. 149.

Recognition characters.—Front of carapace with three teeth each in form of equilateral triangle; rostrum usually a little wider at base, compressed and sometimes slightly longer than orbital teeth. Eyes completely covered by large orbital hoods. Basal article of antennular peduncle with stylocerite reaching to distal third of second article; third article half length of second; second of intermediate length; inner flagellum filiform, outer flagellum thickened proximally. Antennal scale narrow, inner edge regularly curved; lateral spine a little longer than antennular peduncle, separated from and exceed-

ing lamella; basicerite reaching to distal end of basal antennular article, above it a prominent secondary spine.

First legs chelate, unequal, thicker in male than in female. Large chela ovoid; palm about 2.5 times length of fingers, anterior dorsal margin with a strong, sharp tooth at inner side and a blunter tooth on lateral and ventral side near base of dactyl; dactyl broad, larger than immovable finger, tip obtuse, cutting edge a little sinuous, a large tooth at base, dorsal edge curved distally; immovable finger with tip nearly straight, inner edge a little sinuous. Smaller chela elongate, slender, about one-third length of larger; fingers a little shorter than palm, with tufts of hair, acute at tips and curved a little downward; palm narrowly elliptical, surface plain. Second legs slender, weakly chelate; carpus subdivided with joints diminishing as follows (numbered from proximal end): 1, 5, 2-3-4.

Telson with sides slightly sinuous, tip broadly rounded; two pairs of dorsal spines, first pair at about midlength, second pair at about three-fourths length; distal margin with a pair of spines at each posterolateral corner. Uropodal exopods with lateral margin ending in notch armed with two spines separated by a longer movable spine.

Measurements.—Length of body: female, 35 mm.

Color.—Body translucent, yellowish white; large chela white or translucent gray, fingers orange, tips red; banded near base of fingers with white in female, white tipped with green in male.

Habitat.—Lives in dead corals and commensally in sponges; shallow water to 37 fathoms.

Type locality.—Southern [United] States.

Known range.—Near Cape Hatteras, N.C., through West Indies to Alagoas, Brazil; Bermuda.

Remarks.—A number of authors, among them Hay and Shore (1918) and Verrill (1922), have pointed out that Brooks and Herrick (1892) erroneously called *Alpheus normanni* (= *packardii*) by the name *A. minus* in their profusely illustrated monograph. The true *Synalpheus minus* was not treated by them, however, and, at least in the Beaufort, N.C., area, was not available to them in the harbor area studied.

A long breeding season is indicated for this species. Ovigerous females have been taken from

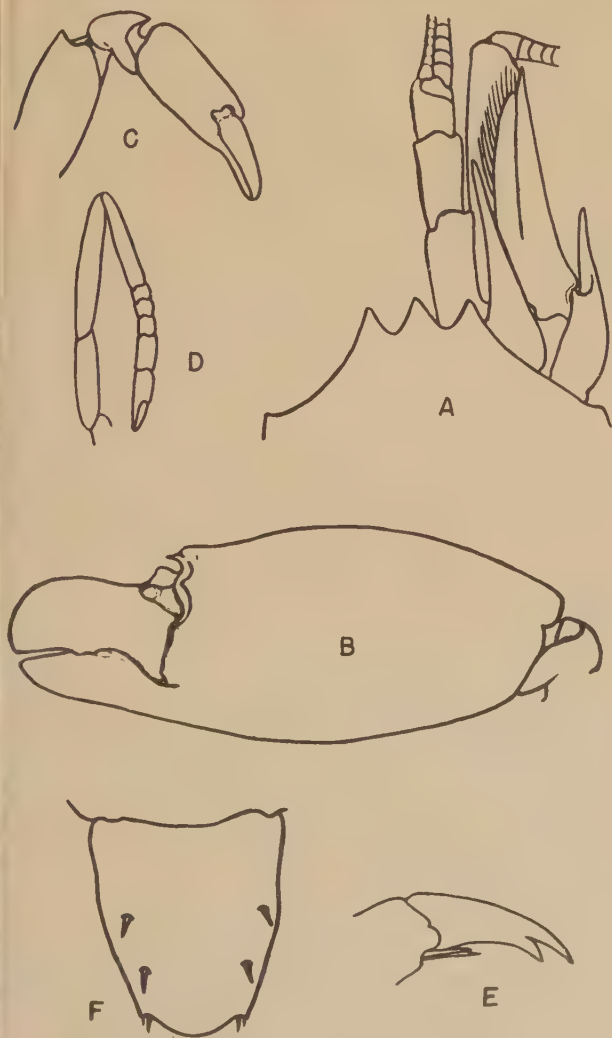


FIGURE 57.—*Synalpheus minus* (Say). A, anterior part of body in dorsal view, with appendages of right side; B, large chela; C, small first cheliped; D, second leg showing subdivided carpus; E, dactyl of third leg; F, telson in dorsal view (after Coutiere, 1909).

February to November in various localities from North Carolina to the Gulf coast; in April in Bermuda; and September in Venezuela. Adults usually occur in pairs (Wass, 1955).

Synalpheus townsendi Coutiere. Small snapping shrimp

Figure 58

Synalpheus townsendi Coutiere, 1909, p. 32, figs. 14–17; Hay and Shore, 1918, p. 384, pl. 26, fig. 1 (rev.).—Verill, 1922, p. 100 (rev.).

Recognition characters.—Rostrum slender, 1.5 times as long as lateral teeth and reaching usually to end of proximal third of second article of antennular peduncle, armed with a ventral prolongation embracing ocellary beak. Teeth on orbital hoods slender; eyes completely covered by hoods. Basal antennular article with stylocerite reaching about as far as rostrum; third article about half length of second; inner flagellum filiform, outer flagellum thickened proximally, bifurcate beyond fourth joint. Antennal scale with strong, slender lateral spine separated from and exceeding lamella distally, spine reaching about to or beyond end of antennal peduncle; basicerite well developed, angled above but lacking dorsal spine, extremity reaching to distal third of basal antennular article.

First pair of legs chelate, very unequal. Large chela with a small, acute dorsal spine at distal margin of palm; upper margin of dactyl elevated into a thick crest; carpus small, irregularly shortened; merus with dorsolateral margin convex, ending in a hooked spine. Small chela one-third length of large one; no brush of hairs on dactyl. Second pair of legs slender, weakly chelate; carpus subdivided, first joint longer than others combined. Third to fifth legs with bifurcate dactyls, both hooks nearly parallel, ventral one narrower and much shorter than dorsal.

Abdomen compressed. Telson with sides somewhat convergent; posterior angles sharp and each provided with a pair of spines, inner spine longer than outer; two pairs of strong dorsal spines, first pair at one-third, second at two-thirds length. Uropods ovate, exopod with lateral margin ending in a notch with a strong fixed spine at its outer and inner angles, between these spines a longer movable spine.

Measurements.—Length of body: ovigerous females, 13 mm.

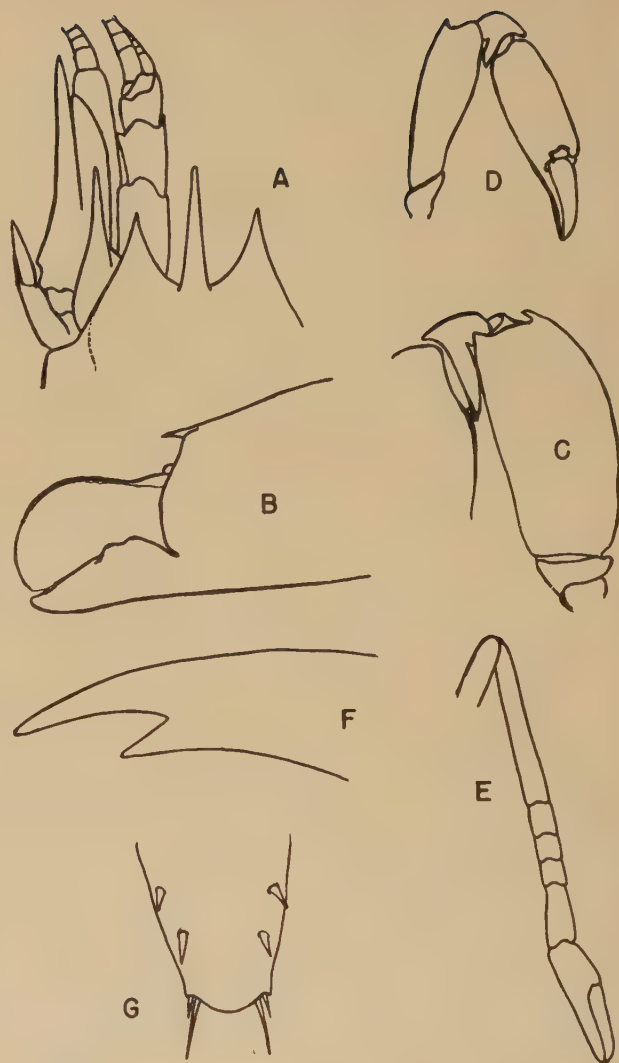


FIGURE 58.—*Synalpheus townsendi* Coutiere. A, anterior part of body in dorsal view, with appendages of left side; B, tip of large chela; C, large cheliped, merus, carpus and proximal end of propodus; D, small first cheliped; E, second leg showing subdivided carpus; F, dactyl of third leg; G, telson in dorsal view (after Coutiere, 1909).

Variations.—The rostrum is variable in length, often shorter than as described above.

Color.—Body and legs translucent pinkish red; large chela pink, changing to green on fingers.

Habitat.—Often found in large sponges; low tide mark to 56 fathoms.

Type locality.—Gulf of Mexico, Albatross station 2373.

Known range.—Off Beaufort, N.C., to Yucatan; through West Indies to Bahia, Brazil; Bermuda.

Remarks.—This species has been taken from offshore reefs in North Carolina at depths of 7 to 8 fathoms (Pearse and Williams, 1951), and from sponges at depths of 16 to 20 fathoms. Wass (1955) remarked that the species seems less dependent on sponges than other members of the genus taken in the Alligator Harbor area of Florida.

Ovigerous females have been taken from the Carolinas in February and August; Obregon, Mexico, in July and August; and Venezuela in September.

Synalpheus longicarpus (Herrick)

Figure 59

Alpheus saulcyi var. *longicarpus* Herrick [in part], 1892, p. 383.

Synalpheus longicarpus: Hay and Shore, 1918, p. 383, text-fig. 6; pl. 26, fig. 2 (rev.).—Verrill, 1922, p. 113, pl. 25, figs. 1a–1h; pl. 34, figs. 3, 3c; pl. 36, figs. 5, 5a (rev.).

Recognition characters.—Rostrum carinate, slender, and slightly longer than triangular, obtuse orbital hoods, reaching about to middle of basal antennular article; space between rostrum and hoods U-shaped, broadest in females. Eyes small, completely covered. Basal article of antennular peduncle with short stylocerite reaching to distal third of article; second article one-third longer than third article; inner flagellum filiform, outer branching at seventh joint, thickened proximally. Terminal article of antennal peduncle exceeding antennular peduncle; antennal scale with strong terminal spine separated from and exceeding rudimentary lamella distally; spine variable in length, often exceeding antennular peduncle by half length of distal article; lamella of scale rudimentary in males, small and variable in females; basicerite slender, acute, with an angle but no accessory spine above, tip reaching to end of second article of antennular peduncle.

First legs chelate, very unequal. Large chela elongate, somewhat ovate, about 2.75 times longer than broad; margins somewhat convex; posterior end swelled and produced backward beyond articulation with small, short carpus inserted below central axis of palm; anterior dorsal margin of palm with small, acute spine near base of dactyl; dactyl somewhat oblique at end, toothed at base,

about one-fourth to one-fifth length of chela. Small chela elongate, about one-third length of larger; dactyl elongate, gently arched dorsally, a dense tuft of erect hairs on dorsal surface along most of length, cutting edge nearly straight with two apical teeth; immovable finger with three teeth, apical one stronger. Second pair of legs slender, weakly chelate; stronger in male than in female; carpus subdivided, first joint shorter than

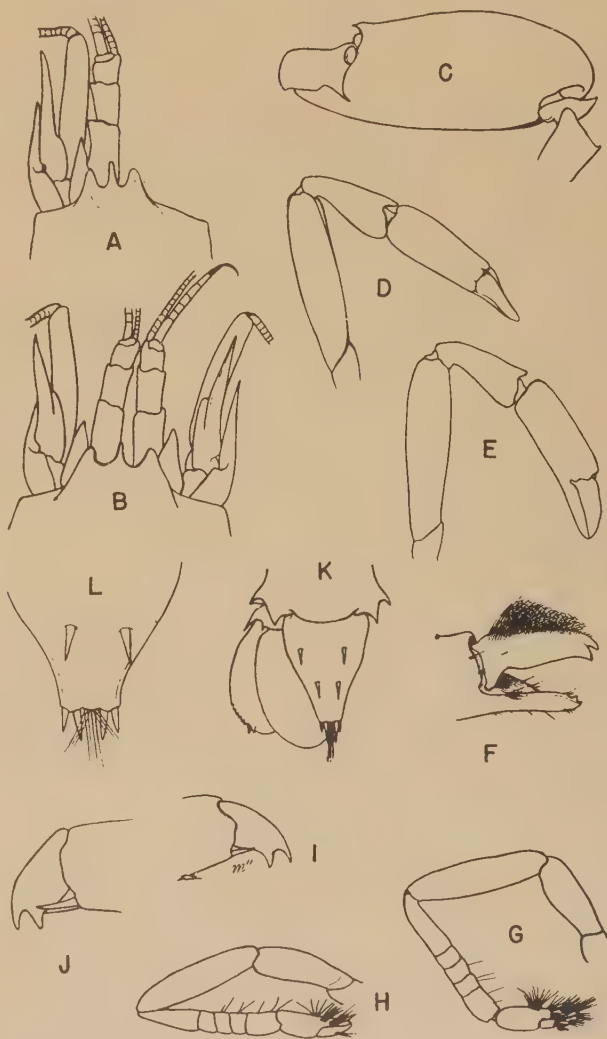


FIGURE 59.—*Synalpheus longicarpus* (Herrick). Anterior part of body in dorsal view, A, male, B, female; C, large chela; D, small first cheliped, male; E, same, female; F, fingers of small first cheliped; G, second leg of male showing subdivided carpus; H, same, female; I, dactyl of third leg; J, same in large adult; K, telson and left uropods in dorsal view, female; L, tip of telson (after Contiere, 1909).

sum of remaining four. Third to fifth legs with dactyls bifurcate.

Sixth abdominal segment with a strong triangular tooth on each posterior angle. Telson with sinuous sides tapering to subtruncate tip; dorsal spines strong, first pair at one-third, second at two-thirds length; tip with two pairs of strong spines, inner pair slightly longer. Uropodal exopod broadly oval; lateral border spined with seven or eight denticles, a movable spine at distal end of series.

Measurements.—Length of body: ovigerous females, 16 to 22 mm.

Variations.—Length of the carpus of the small claw varies with age. The rostrum and projections on the orbital hoods may be entirely lacking or their relative lengths may vary (Wass, 1955).

Color.—Translucent white; fingers brown.

Habitat.—Lives at depths of 15 to 28 fathoms in interior of sponges; especially abundant in *Spheciospongia* (= *Spirastrella*) (Wells, Wells, and Gray, 1960). Sometimes found in sponges cast on beach during storms at Beaufort, N.C.

Type locality.—Specimens upon which Herrick's description is based were taken in the Bahamas, probably at Nassau, New Providence Island.

Known range.—Beaufort, N.C., to Yucatan, Mexico; through West Indies to Curaçao.

Remarks.—This species is common in the Carolinas and often occurs in enormous numbers in the canals of large sponges. Infestation by parasitic isopods is common, *Phryxus subcaudalis* Hay occurring on the surface of the abdomen and *Synsynella deformans* Hay in the branchial chambers.

Ovigerous females have been taken off North Carolina in August and December. The species hatches in essentially the adult form (Herrick, 1892). Coutiere (1909) and Wass (1955) remarked on the fact that few ovigerous females occur among crowded populations in sponges.

Family Ogyrididae

Caridea with first two pairs of legs chelate, nearly equal in size and not much if any larger than other legs. Carpus of second legs subdivided. Rostrum small or wanting. Eyestalks long, slender, fully exposed but with corneal surface reduced. Telson thick, obtusely pointed. Blades

of uropods curved outward. Thelycum present in females (Hay and Shore, 1918).

Genus *Ogyrides* Stebbing, 1914

Stebbing, 1914, p. 31; Hemming, 1958b, p. 158.

KEY TO SPECIES IN THE CAROLINAS

- a. Postrostral crest with 8 to 14 small, fixed spines
limicola (p. 74).
- aa. A single movable spine behind rostrum on middorsal line.....*alphaerostris* (p. 75).

Ogyrides limicola Williams

Figure 60

Ogyrides limicola Williams, 1955c, p. 57, fig. 1.

Recognition characters.—Rostrum short, depressed, equilaterally triangular. Postrostral carina with 8 to 14 teeth, flanked on each side by row of setae extending to tip of rostrum. Pterygostomian area broadly obtuse. Eyestalks long, lightly setiferous dorsally and dorso-medially, narrowest in middle, exceeding antennular peduncles by approximately 2.5 times corneal length. Antennal and antennular peduncles nearly equal in length; second antennular article 3 times as long as third article; stylocerite of basal article terminating in two strong acuminate spines of nearly equal length. Antennal scale and second article of antennular peduncle reaching nearly same level distally; scale evenly

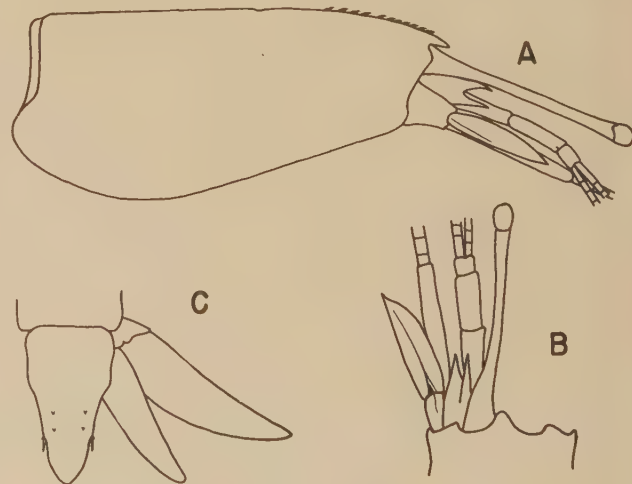


FIGURE 60.—*Ogyrides limicola* Williams. A, carapace and anterior appendages in lateral view; B, anterior appendages and portion of carapace in dorsal view; C, telson and uropods of right side in dorsal view; A-C approximately $\times 10$ (after Williams, 1955c).

rounded medially, 3 times longer than greatest width, greatest width in basal half. Third maxilliped, when extended, exceeding eyestalks.

First legs exceeding midlength of antennal peduncle by full length of chelae; fingers of chelae pointed, agape when closed.

Telson with anterior pair of spines placed well behind lateral prominences. Uropods with exopods slightly falciform, lateral borders nearly straight. Telson with three horny ridges at proximolateral corners ventrally, and uropods with an interlocking horny eminence on basal article dorsally.

Measurements.—Length of body: ovigerous holotypic female, 16 mm.

Variations.—Individual variations are shown in the number of spines on the postrostral crest and in the lengths of the spines of the stylocerite.

Color.—Female with general body structure colorless, clear; internal organs visible; gut dark; hepatopancreas light brown; eyestalks, antennal and antennular peduncles, and distal portions of anterior appendages with red and yellow spots; uropods and sixth segment of abdomen with scattered red spots. Ovigerous females with yellow green (chartreuse) colored eggs on swimmerets (Williams, 1955c).

Habitat.—On (or in) the bottom of muddy estuaries, or in plankton; surface to 2.5 fathoms. Collections have been made in an observed bottom salinity range of 9 to 31‰, but salinities in sounds near inlets often range higher than this.

Type locality.—Mouth of Far Creek at Engelhard, Hyde County, N.C.

Known range.—Eastern shore of Accomac County, and lower James River, Va., to Lake Pontchartrain, La.

Remarks.—The systematic confusion surrounding the two species *O. alphaerostris* and *O. limicola* was discussed by Williams (1955c). The two species are quite distinct morphologically and differ in total size, *O. limicola* being the smaller. The latter occurs most frequently in collections from estuaries. Young specimens have frequently been taken in plankton tows made at night in Bogue Sound, N.C., but adults are seldom taken by this method of collection. Occurrence of adults in samples taken with a beam trawl suggests burrowing habits similar to those described for *O. alphaerostris*, but in muddier situations and

often in low salinities. The type locality and a number of other productive collecting spots in North Carolina are shallow, mud-bottomed, non-tidal estuarine streams.

In North Carolina, collections of *O. limicola* have been made in all seasons of the year, and ovigerous females have been taken from May to September.

Ogyrides alphaerostris (Kingsley)

Figure 61

Ogyris alphaerostris Kingsley, 1880, p. 420, pl. 14, fig. 7.
Ogyrides alphaerostris: Stebbing, 1914, p. 31.—Hay and Shore, 1918, p. 388, fig. 11, pl. 26, fig. 9.

Recognition characters.—Rostrum depressed, equilaterally triangular, tipped with setae. A single, postrostral, movable spine. Pterygostomian area obtuse. Eyestalks long, setiferous medially, narrowest in middle, exceeding antennular peduncle by approximately twice corneal length. Antennal and antennular peduncle nearly equal in length; second article of antennular peduncle slightly over twice as long as third article;

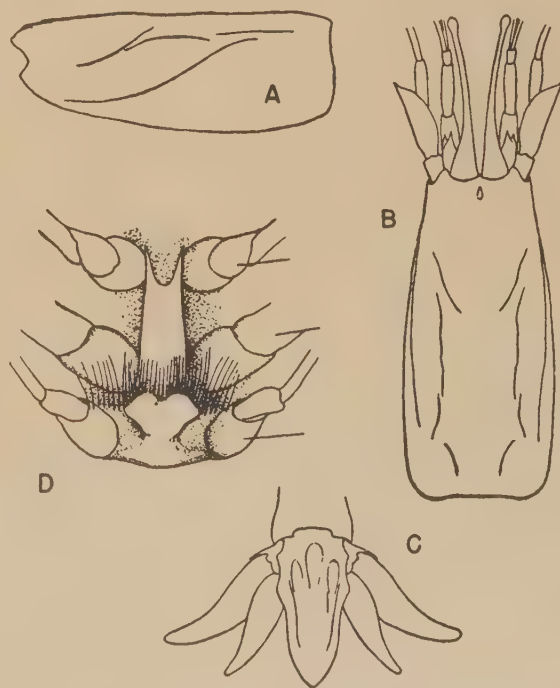


FIGURE 61.—*Ogyrides alphaerostris* (Kingsley). A carapace in lateral view; B, carapace and anterior appendages in dorsal view; C, uropods and telson in dorsal view; D, sterna of last three thoracic segments showing thelycum of female; A–C female $\times 5$, D $\times 7.8$ (after Hay and Shore, 1918).

stylocerite terminating in two acuminate spines; lateral spine longer. Antennal scale and second article of antennular peduncle reaching same level distally; scale evenly rounded medially, approximately three times longer than greatest width, greatest width near base. Third maxilliped, when extended, exceeding eyestalks.

First legs scarcely extending to tip of antennal scale. Second legs exceeding antennal scale by full length of chelae; fingers of chelae pointed, agape when closed.

Telson with anterior pair of spines placed approximately at level of lateral prominences. Uropods with exopods somewhat falciform, curvature greatest distally. Telson with three horny ridges at proximolateral corners ventrally, and uropods with an interlocking horny eminence on basal article dorsally.

Measurements.—Length of body: ovigerous female, 27 mm.

Color.—Body nearly transparent; red and green spots or flecks on eyestalks, antennules, and antennae; green only on distal joints of third maxillipeds; red only on basal articles of legs, on first pleopods, at bases of all pleopods, and on abdominal pleura and sterna; a conspicuous red area on sixth abdominal segment distoventrally and another around mouth.

Habitat.—Often found on firm bars of sand just offshore along open ocean in water 1 m. deep (Pearse, Humm, and Wharton, 1942); surface to 5 fathoms.

Type locality.—Eastern shore of Northampton County, Va.

Known range.—Northampton County, Va., to St. Simons Island, Ga.; Alligator Harbor, Fla., to Horn Island, Miss.

Remarks.—*Ogyrides alphaerostris* apparently is more restricted to high-salinity waters than *O. limicola*, for it has seldom been collected in the sounds of North Carolina and then only near inlets. Pearse, Humm, and Wharton (1942) described burrowing habits of the species on sandy bars and commented that members of the genus are unusual in that they have long eyestalks like *Uca*, yet are burrowers. *Ogyrides alphaerostris* burrows forward (head first), using the third maxillipeds and legs for digging and propulsion. Sand is pushed upward and over the head, the abdomen often being left above sand for a time,

especially in ovigerous females. The fifth leg is held high on the sides and stroked dorsally and posteriorly, legs one to four are stroked laterally and posteriorly, and the third maxillipeds moved anteriorly and dorsally. The animals scrape food from the antennae with setose mouth parts.

Ovigerous females have been taken in July in North Carolina, and in July and August in Florida and Mississippi. The above authors imply that the breeding season is extended through the summer months.

Family Hippolytidae

Caridea with first two pairs of legs chelate, first pair not much stronger than rest; carpus of second pair of legs subdivided. Eyes well developed and not covered by carapace. Mandibles usually deeply cleft. Second maxillipeds with a very short dactyl.

KEY TO GENERA AND SOME SPECIES IN THE CAROLINAS

- a. Carpus of second legs with three to five joints.
 - b. Carpus of second legs with five joints
 - Thor floridanus* (p. 76).
 - bb. Carpus of second legs with three joints.
 - c. Series of small spines (five to nine) along anterior margin of carapace below eye
 - Latreutes* (p. 78).
 - cc. Without series of small spines on anterior margin below eye.
 - d. Rostrum shorter than carapace proper, with spines above and below ----- *Hippolyte* (p. 80).
 - dd. Rostrum nearly twice length of carapace proper, smooth above, serrate below
 - Tozeuma carolinense* (p. 83).
- aa. Carpus of second legs with more than six joints (multiarticulate) ----- *Hippolytasmata* (p. 84).

Genus *Thor* Kingsley, 1878

Kingsley, 1878b, p. 94.—Hemming, 1958b, p. 161.

Thor floridanus Kingsley

Figure 62

Thor floridanus Kingsley, 1878b, p. 95.—Verrill, 1922, p. 136, pl. 35, figs. 2-2f; pl. 41, fig. 1; pl. 46, figs. 2-2e; pl. 47, figs. 4, 4a.—Holthuis, 1947, p. 47, 49 (rev.).

Recognition characters.—Rostrum shorter than eyes; dorsal margin with four or five teeth, first tooth a little behind margin of orbit, distal tooth near tip making tip appear bifid; ventral margin unarmed. Carapace smooth, with prominent antennal spine below orbit. Eyes well developed. Antennules with basal article large; stylocerite long, acute, reaching beyond tip of basal article

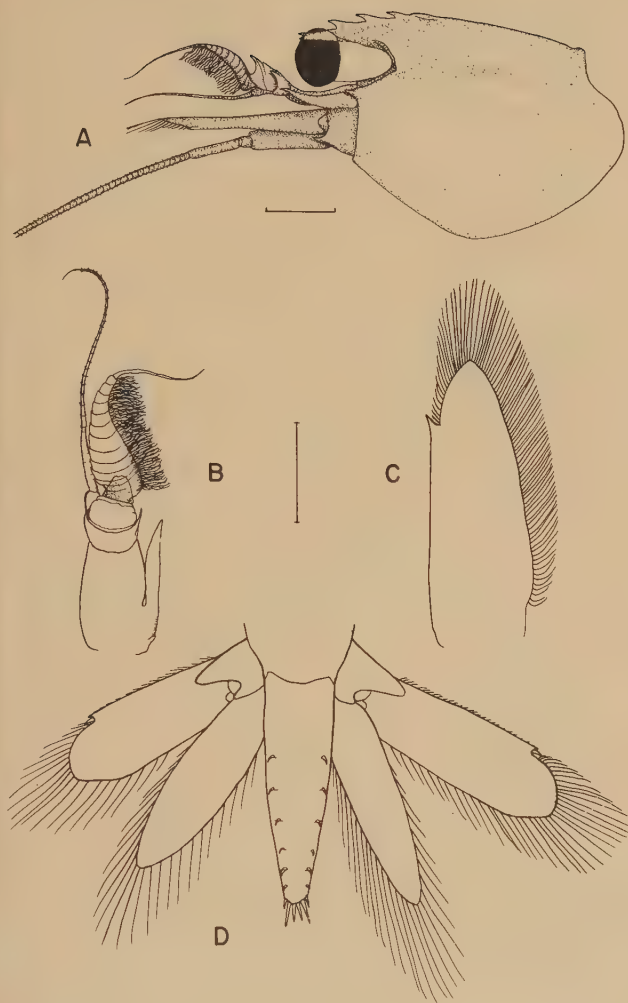


FIGURE 62.—*Thor floridanus* Kingsley. A, carapace and anterior appendages in lateral view, 1 mm. indicated; B, antennule; C, antennal scale; D, uropods and telson; B–D, 1 mm. indicated.

to level of tip of spine on second article; a tiny, erect spinule at base of stylocerite; second and third articles short; second with slender, acute spine on lateral surface; third with a thin, flat, blunt projection on upper side; inner flagellum slender, slightly longer than peduncle; outer flagellum stout basally, tapering abruptly to thin terminal portion, densely hairy on outer margin, about as long as peduncle. Antennal scale with outer margin nearly straight, terminating in a stout spine, lamella exceeding spine, an outer spine near base of scale. Third maxilliped reaching a little beyond tip of antennal scale; last article terminating in slender spines.

First legs with merus and carpus subequal; carpus with minute spinules on inner margin; chelae subcylindrical, dactyl two-fifths total length of hand. Second legs with carpus subdivided into six joints of varying lengths; chela as long as fifth and sixth carpal joints. Dactyls and propodi of third to fifth legs spinulose beneath; dactyls bifurcate but with accessory spines proximally.

Abdomen smooth; pleura of fourth, fifth, and sixth segments with posterolateral angles acute. Telson elongate, triangular, with five prominent pairs of dorsal spines a little remote from edges and spaced equidistantly in posterior three-fourths of length; tip somewhat rounded and armed with three pairs of subequal spines, outer pair shortest. Uropodal exopods with outer edge ending in a small spine flanked medially by a strong movable spine.

Measurements.—Length of body: ovigerous females, 11 to 13 mm. (Wass, 1955).

Habitat.—Among sponges, ascidians, algae, and soft corals; shallow water to 32 fathoms.

Type locality.—Key West, Fla.

Known range.—Beaufort, N.C., to Alabama; through West Indies to Curaçao and Yucatan; Bermuda.

Remarks.—This species has often been referred to *Thor paschalis* (Heller), an Indo-west Pacific form. Holthuis (1947) considered the West Indian species distinctive, and, in fact, it is the type species of the genus. As far as known, *T. floridanus* is not common in the Carolinas.

Ovigerous females have been reported (Broad, 1957c; Lunz, 1939; Verrill, 1922; Wass, 1955) or are known from collections from April to August in southeastern United States, Bermuda, and the West Indies. In addition, they are known from Cuba in November and January.

Broad (1957c) worked out the larval stages of this form, using various species of algae as food for the developing larvae. Though survival varied with species of algae fed, he considered at least certain species of algae to be an adequate diet for survival, molting, and metamorphosis. Broad described eight zoeal stages and a postlarval stage. Comparison of these stages with earlier descriptions by Lebour (1940) led Broad to question the conspecificity of *Thor* from Bermuda and the Carolinas.

Genus *Latreutes* Stimpson, 1860

Stimpson, 1860, p. 27.—Hemming, 1958b, p. 157.

KEY TO SPECIES IN THE CAROLINAS

- a. Carapace and rostrum unarmed dorsally except for a single, small, median spine on gastric region; rostrum an elongate blade nearly as long as carapace *fucorum* (p. 78).
- aa. Carapace strongly humped and armed dorsally with five or six spiniform teeth; rostrum a deep ovoid blade, shorter than carapace-----*parvulus* (p. 79).

Latreutes fucorum (Fabricius)

Figure 63

Palaemon fucorum Fabricius, 1798, p. 404.

Latreutes ensiferus: Hay and Shore, 1918, p. 390, pl. 26, fig. 13.

Latreutes fucorum: Verrill, 1922, p. 131, pl. 16, figs. 5-5b; pl. 42, figs. 2-2t; pl. 44, figs. 1-1m, 2a-2n, 3 (rev.).

Recognition characters.—Rostrum thin, nearly as long as carapace, smooth edged, broadest at base and deepest near base, slightly concave dorsally and upturned at tip, convex ventrally; tip subtruncate and armed with about five to seven small, acute spinules. Carapace smooth; a small middorsal spine on gastric region; anterior margin produced into an acute lobe below eye followed ventrally by a wide, nearly rectangular emargination and a series of four to nine small denticles at anterolateral angle; a spine removed from margin near suborbital lobe. Eyes well developed, with a tuberculate swelling antero-medially near cornea. Antennular peduncle with basal article excavate laterally; stylocerite broad, thin, cupped dorsally; distal spine on lateral border of basal article reaching about to base of third article; second and third articles short; distal border of third obscurely denticulate, outer flagellum thick at base. Antennal peduncle stout; antennal scale wide at base, tapering to acute terminal spine, scale about as long as rostrum. Third maxilliped elongated, leglike; distal article long, with eight or nine acute marginal spines.

First legs incurved, short, relatively stout, unequal; larger chela thick, proximally broad, ovate, tapering distally; dactyl wide, longer than immovable finger, with broad lateral lobe and about three denticles at tip; immovable finger bent slightly inward and arched, tip subacute or slightly bidentate; fingers hairy; carpus large, cup-shaped, broader than long; merus and carpus excavate beneath. Second legs slender; chelae slender, somewhat unequal; fingers about as long as palm,

hairy at tip; carpus with three unequal joints, middle one longest. Third to fifth legs long, slender, subequal; propodi and dactyls with row of spines on lower edge.

Abdomen smooth. Telson long, narrow, tapering to narrow tip with spiniform median process flanked by two pairs of unequal spines, inner pair longer than median process; two pairs of dorsal spines, at half and three-fourths of length. Uropodal exopods with outer edge terminating in a small spine flanked medially by a movable spine.

Measurements.—Length of body: adults, 12 to 20 mm.; males smaller than females.

Variations.—The rostrum varies greatly in length, depth, and number of spines (Wass, 1955).

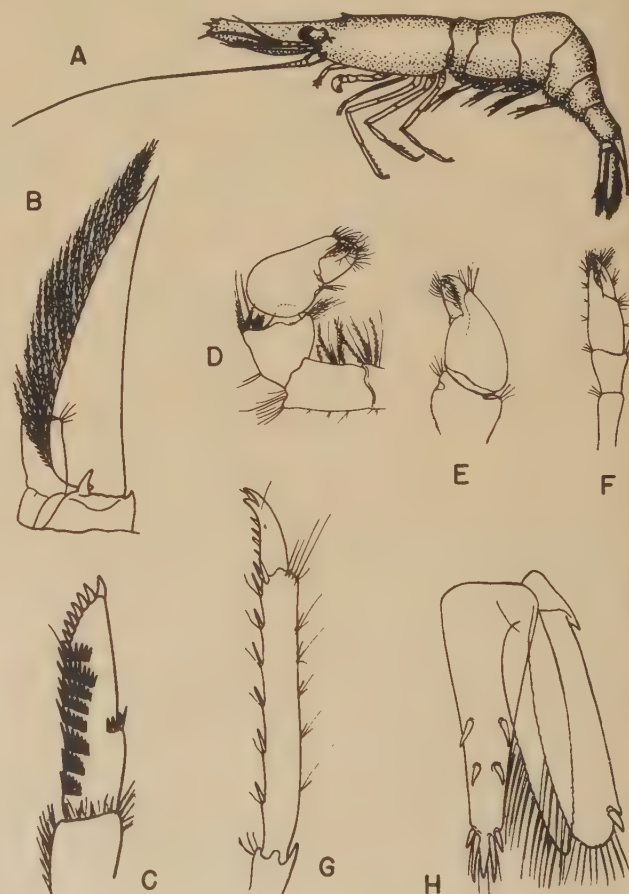


FIGURE 63.—*Latreutes fucorum* (Fabricius). A, animal in lateral view, $\times 17$ (after Bate, 1888); B, antennal scale, $\times 17$; C, distal article of third maxilliped, $\times 42$; D, right first cheliped, $\times 17$; E, left first cheliped, $\times 25$; F, second cheliped, $\times 17$; G, distal articles of third leg, $\times 17$; H, telson and uropods, $\times 17$ (after Verrill, 1922).

Color.—Often nearly colorless and transparent; sometimes with body pale yellow, yellowish green, greenish brown, brown, red, black, black with white spots and bars; bright blue patches on dorsal and lateral surfaces; often mottled, striped, or barred, and corresponding in pattern to irregularly colored bits of weed (various authors).

Habitat.—Common in floating masses of *Sargassum*; surface waters.

Type locality.—Floating gulfweed.

Known range.—Newfoundland to Puerto Rico, through Gulf of Mexico to Texas; Bermuda; near the Azores and Cape Verde Islands; Cape of Good Hope (?) (Holthuis, 1951b; Sivertsen and Holthuis, 1956).

Remarks.—Ovigerous females have been observed in inshore waters of the Carolinas and adjacent western Atlantic region from July to October. They have been observed in the Gulf of Mexico from April to June. In the middle and western Atlantic they have been observed in June (Sivertsen and Holthuis, 1956). Gurney (1936a) described the first stage larva.

Pearse (1952b) reported the parasitic *Probopyrus latreuticola* (Gissler) in the gill cavity of this shrimp near Port Aransas, Texas.

Brown (1939) found four kinds of pigment in this shrimp (white, red, yellow, and blue) similar to pigments found in *Hippolyte*, *Leander*, and *Palaemonetes* species. The red and yellow pigments respond to white background by concentration into the chromatophore centers and to black background by dispersion into the chromatophore branches. *Latreutes* has a great abundance of white pigment which may vary in color from yellowish white to clear white. Darkness produces concentration, and darkness or black background with low intensity of incident light calls forth concentration of the reflecting white chromatophores. Direct sunlight of a bright sky produces dispersion of white pigment in spite of black background. Blue patches on the animals apparently consist of blue pigment accumulated in particular white chromatophores. Brown concluded that the different color patterns in this species are not solely results of responses to particular situations, but are at least partly genetic patterns repressed or encouraged by light intensity in color of the background. The re-

sponse is similar to responses in crustaceans having far less ability to change color.

Latreutes parvulus (Stimpson)

Figure 64

Rhynchocyclus parvulus Stimpson, 1866, p. 48.—1871b, p. 124.
Concordia gibberosus: Hay and Shore, 1918, p. 391, pl. 26, fig. 11.

Latreutes parvulus: Holthuis, 1947, p. 59.—1951b, p. 131, fig. 28 (rev.).

Recognition characters.—Rostrum laterally compressed, almost circular in outline in female, more elongate in male; upper margin with six to eight teeth in female, two to four in male; a few small teeth on tip; lower margin unarmed or with up to five shallow teeth; ventral part of rostrum produced somewhat backward. Carapace

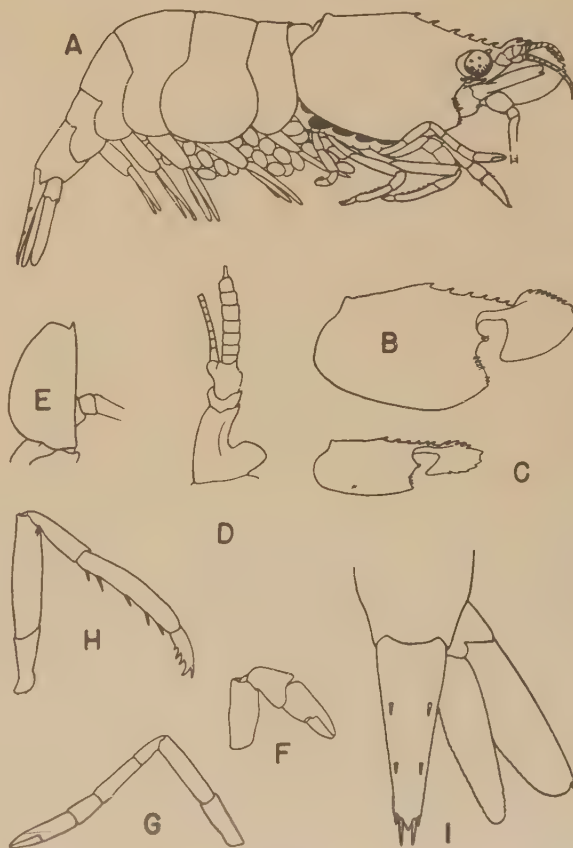


FIGURE 64.—*Latreutes parvulus* (Stimpson). A, ovigerous female in lateral view, $\times 6$; B, carapace of ovigerous female in lateral view, $\times 6$; C, carapace of male in lateral view, $\times 6$; D, antennule, $\times 13$; E, antennal scale, $\times 13$; F, first leg, $\times 17$; G, second leg, $\times 17$; H, third leg, $\times 17$; I, telson and right uropod in dorsal view, $\times 17$ (after Holthuis, 1951b).

with middorsal row of five to seven small, erect teeth, row starting somewhat anterior to middle of carapace, extending to base of rostrum; carapace somewhat swollen in female, making an angle at base of middorsal row of teeth; upper margin nearly straight in males; anterior margin with a narrow, anteriorly directed lobe forming lower angle of orbit, a slender spine on lobe; anterolateral angle serrate with two to four teeth; between anterolateral angle and lower margin of orbit a row of three or four slender spines a bit removed from and parallel to margin. Eyes well developed; cornea globular; eyestalk with a truncated process at upper inner margin overlapping line separating cornea from stalk. Antennular peduncle with stylocerite broad and rounded, hollowed above and together with basal article of peduncle forming concavity for reception of eye; second article of peduncle much shorter than third; upper flagellum shorter than lower, with seven or eight broad and one or two narrow joints. Antennal scale about twice as long as broad, overreaching antennular and antennal peduncles, but not reaching end of rostrum; outer margin nearly straight, ending in a small tooth reaching about as far as lamella; a small spine on outer surface of peduncle near base of scale.

First legs equal, short, thickset, slightly overreaching base of antennal scale; fingers somewhat shorter and narrower than palm, tips of fingers ending in dark-colored nails; palm broadened posteriorly; carpus somewhat conical, about as long as palm. Second legs more slender, reaching about to end of antennal peduncle; chelae with fingers shorter than palm; carpus almost twice length of chela, three-jointed, median joint longest; merus two-thirds as long as carpus. Third to fifth legs with dactyls ending in a sharp tooth, posterior margin with four comblike teeth progressively smaller proximally.

Abdomen smooth. Telson triangular; with two pairs of dorsal spines at half and three-fourths length; tapering to a narrow tip with spiniform median process flanked by two pairs of spines, inner pair longest; terminal portion with feathered setae. Uropodal exopods with outer margin ending in a small spine flanked medially by a movable spine.

Measurements.—Length of body: 7 to 12 mm.; males smaller than females.

Variations.—Shape of the rostrum, as well as its spination, is subject to some variation.

Habitat.—Littoral waters from (in?) sponges, and among shells and hydroids; surface to 24 fathoms.

Type locality.—St. Joseph Island, Tex.

Known range.—Beaufort, N.C., to Texas; Cuba; Puerto Rico; French Guiana; Rio de Janeiro, Brazil; Sierra Leone, West Africa.

Remarks.—For many years this species has been known as *Concordia gibberosus* Kingsley or *Latreutes gibberosus* (Kingsley). Holthuis (1947) showed that these names fall into the synonymy of Stimpson's species.

Latreutes parvulus is not known to be common anywhere in its range. It has been taken throughout the year in the Carolinas. Ovigerous females have been taken throughout the year in various parts of the range north of the equator and in February in Brazil.

Genus *Hippolyte* [Leach, 1814]

Verrill, 1922, p. 124.—Holthuis, 1947, p. 53.—Hemming, 1958b, p. 157.

KEY TO SPECIES IN THE CAROLINAS

- a. Basal article of antennular peduncles without distal spines dorsally-----*pleuracantha* (p. 80).
- aa. Basal article of antennular peduncles with distal spines dorsally-----*zostericola* (p. 82).

Hippolyte pleuracantha (Stimpson)

Figure 65

Virbius pleuracanthus Stimpson, 1871b, p. 127.

Hippolyte pleuracantha: Hay and Shore, 1918, p. 390, pl. 26, fig. 8.—Holthuis, 1947, p. 15 (rev.).

Recognition characters.—Body smooth, with tufts of plumose hairs on dorsal surface of carapace and abdomen, tips of abdominal pleura, and distal portion of eyestalks. Rostrum rather stout at base, thin distally, slightly decurved, armed dorsally with one to three teeth and ventrally with one to three teeth near tip; tip reaching about to end of antennular peduncle; a strong spine on each side at base of rostrum. Anterior margin of carapace produced into a lobe below eye followed ventrally by an antennal spine, an emargination at base of antenna followed by a slightly produced, broadly rounded anterolateral angle; hepatic spine strong. Eyes well developed. Antennular peduncle with basal article long and broad, stylocerite slender, lanceolate, reaching

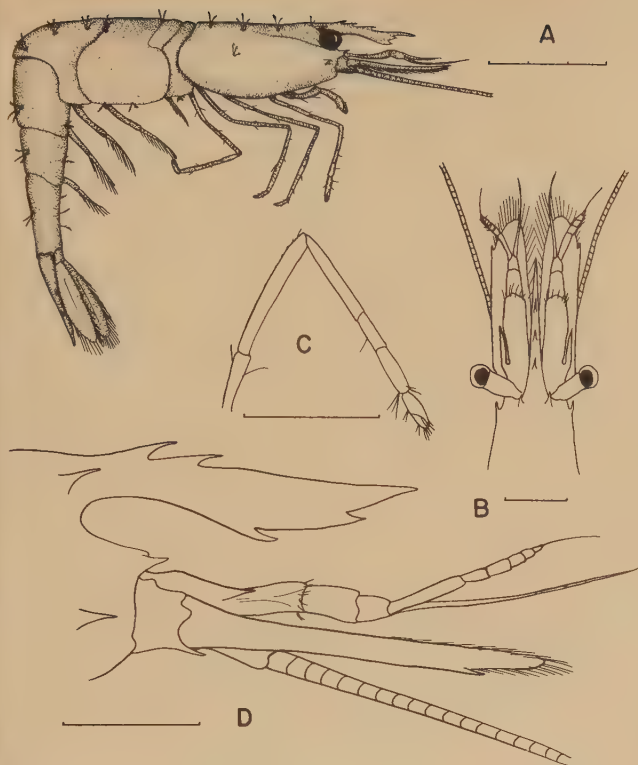


FIGURE 65.—*Hippolyte pleuracantha* (Stimpson). A, animal in lateral view, 3 mm. indicated; B, anterior portion of body in dorsal view; C, second leg; D, anterior portion of body in lateral view; B-D, 1 mm. indicated.

about to middle of article and separated from lateral border of article by about width of stylocerite, article ending in a short, broad, elevated, bladelike projection, a short spine at anterolateral corner under blade; second and third articles much shorter than first; antennular flagella of about equal length; outer ramus stout, broadest in middle, tapering to slender distal portion, hairy on ventral border. Antennal scale large, exceeding rostrum and reaching nearly to end of antennular flagella, length a little over three times width; outer margin slightly concave, terminating in a small spine, spine exceeded by lamella; a spine near base of scale.

First legs short, nearly equal, reaching a little beyond base of distal article of antennal peduncle; chelae setose, palm inflated, fingers about half length of palm, cutting edges finely serrate; carpus irregularly conical in shape, about three-fourths length of chela, lower outer border with spiniform setae. Second legs slender, reaching to

tip of antennular peduncle; carpus longer than merus, divided into three joints; fingers two-fifths length of chelae, tips of cutting edges with spines; chelae hairy. Third to fifth legs long; third reaching to tip of antennal scale; dactyls with series of spines in comblike arrangement on inner border; propodi spined on inner border.

Abdomen strongly bent at third segment; posterior portion of third segment raised with hoodlike projection overhanging fourth segment. Telson with two pairs of dorsal spines on lateral border, one about at half, another at three-fourths length; tip truncate, bearing three pairs of spines, inner two pairs nearly equal, outer pair much shorter. Uropodal exopods with lateral border ending in a small spine flanked medially by a movable spine.

Measurements.—Length of body: ovigerous females, 12 to 18 mm.; males somewhat smaller.

Variations.—The rostrum in this species varies conspicuously in number of teeth, in shape from lateral view, and in length. Dorsal and ventral rostral teeth occur in all combinations from 1/1 to 3/3. Males are more slender than females.

Color.—Usually mottled brown or red, often a bright green.

Habitat.—Extremely abundant in beds of vegetation (*Zostera* and *Diplanthera*) in sounds and bays. Also found among rocks of jetties.

Type locality.—Norfolk Harbor, Va., and Somers Point, Great Egg Harbor, N.J.

Known range. New Jersey to Galveston, Tex.; Bermuda.

Remarks.—The two species, *Hippolyte pleuracantha* and *H. zostericola*, have been much confused over the years, and it is not at all certain that differences pointed out here adequately distinguish them. No attempt has been made here to give complete synonymies. This task must be approached by a thorough revisionary work in which all existing collections are studied.

In general, it can be stated that *H. pleuracantha* has no prominent distal spines on the basal article of the antennular peduncle; it has a relatively shorter rostrum, and appears to be somewhat larger than *H. zostericola*. *Hippolyte zostericola* has a prominent, distal, dorsal pair of spines on the basal article of the antennular peduncle. I am much indebted to L. B. Holthuis for pointing out

the latter character to fellow workers on the American coast.

Because identifications in the literature are probably confused, the geographic limits of the species given here must be regarded with reserve.

Ovigerous females of *H. pleuracantha* occur in North Carolina at least from April to October in the Beaufort area. Gurney (1936b) pointed out some differences between adults of *H. pleuracantha* and *H. zostericola* (as well as other species of *Hippolyte*) and described four larval and two postlarval stages of what he considered to be a Bermudian subspecies, *H. pleuracantha bermudensis*.

***Hippolyte zostericola* (Smith)**

Figure 66

Virbius zostericola Smith, 1873c, p. 550, pl. 3, fig. 11.
Hippolyte zostericola: Holthuis, 1947, p. 16.

Recognition characters.—Body smooth. Rostrum rather stout at base, thin distally, slightly decurved, armed dorsally with three or four teeth and ventrally with two to five teeth distally; tip reaching beyond antennular peduncle and often nearly to tip of antennal scale; a strong spine on each side at base of rostrum. Anterior margin of carapace produced into a prominent narrow lobe below eye followed ventrally by an antennal spine; a shallow emargination at base of antenna and a broadly rounded anterolateral angle; hepatic spine well developed. Antennular peduncle with basal article long and broad, stylocerite slender, divergent at tip and well separated from article, basal article terminating in a pair of well-developed spines on anterolateral corner; second and third articles much shorter than first; antennular flagella of about equal length, outer ramus stout basally, tapering to slender distal portion, hairy on ventral border. Antennal scale large, slightly exceeding rostrum and reaching nearly to end of antennular flagella, length a little over three times width; outer margin slightly concave, terminating in a small spine, spine exceeded by lamella; a spine near base of scale.

First legs short, nearly equal, reaching base of distal article of antennal peduncle; chelae lightly setose, palm inflated, fingers about half length of palm, cutting edges finely serrate;

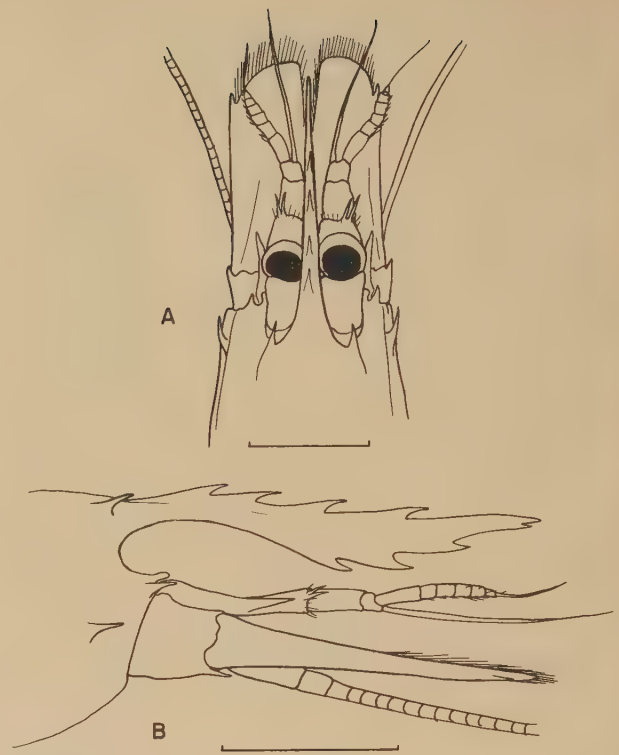


FIGURE 66.—*Hippolyte zostericola* (Smith). A, anterior portion of body in dorsal view; B, anterior portion of body in lateral view; 1 mm. indicated.

carpus irregularly conical in shape, about three-fourths length of chela, lower outer border with spiniform setae. Second legs slender, reaching to distal end of basal article of antennular peduncle; carpus longer than merus, divided into three joints; fingers about two-fifths length of chelae, tips of cutting edges with spines; chelae hairy. Third to fifth legs long; third reaching to tip of antennal scale; dactyls with series of spines in comblike arrangement on inner border; propodi spined on inner border.

Abdomen strongly bent at third segment; posterior portion of third segment raised with hoodlike projection overhanging fourth segment. Telson with two pairs of dorsal spines on lateral border, one at half, another at three-fourths length; tip truncate, bearing three pairs of spines, inner two pairs about equal, outer pair much shorter. Uropodal exopods with lateral border ending in a small spine flanked medially by a movable spine.

Measurements.—Length of body: ovigerous females, 10 to 12 mm.; males somewhat smaller.

Variations.—The rostrum in this species varies considerably in number of teeth, shape from lateral view, and relative length. Dorsal and ventral teeth have been observed in the combinations 3/3, 3/4, 3/5, 4/2, 4/4, and the range of variation may be greater than this because only a few specimens from the Beaufort, N.C., area have been studied. Males are more slender than females.

Color.—Bright green, pale or translucent tinged with green; sometimes specked with reddish brown and with a broad median band of dark brown extending whole length of body (Smith, 1873c).

Habitat.—Beds of vegetation such as eelgrass.

Type locality.—Vineyard Sound, Mass.

Known range.—Southern Massachusetts, through Gulf of Mexico and West Indies to Curaçao (Holthuis, 1947).

Remarks.—Differences between this species and *H. pleuracantha* are discussed in the account for *H. pleuracantha*. Ovigerous females have been found in North Carolina in September.

Genus *Tozeuma* Stimpson, 1860

Stimpson, 1860, p. 26.—Holthuis, 1955, p. 112 (rev.).

Tozeuma carolinense Kingley. Arrow shrimp

Figure 67

Tozeuma carolinensis Kingsley, 1878b, p. 90.—1880, p. 413.—Schmitt, 1935a, p. 155.

Tozeuma carolinense: Rathbun, 1901, p. 114.—Hay and Shore, 1918, p. 391, pl. 27, fig. 2.

Agasia carolinensis: Holthuis, 1947, pp. 17, 61.

Recognition characters.—Body elongate, compressed. Rostrum slender, almost twice as long as remainder of carapace, inclined slightly upward distally, rounded and unarmed dorsally, base somewhat flattened and horizontal, deepest anterior to orbit and decreasingly lamellate distally; ventral border with many appressed teeth. Carapace smooth, polished; a strong spine at either side of base of rostrum; anterior margin produced into a triangular tooth below eye; anterolateral angle with a spine. Eyes well developed. Antennular peduncle rather slender; first article longest, with slender stylocerite slightly exceeding distal border; second and third articles progressively shorter; outer flagellum thick and much shorter than inner, neither quite reaching tip of antennal scale. Antennae longer than rostrum; antennal

scale lanceolate, less than half length of rostrum; basal antennal article with a strong ventrolateral spine on anterior border.

Legs relatively short; first pair very short, stout, hand inflated, fingers curved, closing completely, spines on fingers dark colored; second pair slender, longer, carpus with three joints, proximal joint nearly as long as merus; legs three to five with comblike spines on curved dactyls.

Abdomen smooth; strongly bent between third and fourth segments; third segment of male bearing a low dorsal hump; fifth segment with a spine at each side of posterior border; sixth with a spine at posterolateral angle and a broad spine at base of telson. Elements of tail fan long and narrow. Telson with one pair of dorsal spines at midlength, another at three-fourths length; tip with a strong pair of median spines flanked by a weak lateral pair. Uropodal exopods with outer border terminating in a small spine flanked medially by a movable spine.

Measurements.—Length of body: ovigerous females, 28 to 50 mm.

Variations.—The humped third abdominal segment is pronounced in young individuals of both sexes.

Color.—Apparently varying to some degree depending on background; shades of green from light yellowish green to rich deep green, or occasionally brownish or red in beds of *Diplanthera wrightii* and *Zostera marina* (Bryce, 1961); purple on alcyonarian corals *Antillologorgia* and *Pterogorgia* (Voss, 1956); nearly colorless (Ver-rill, 1922).

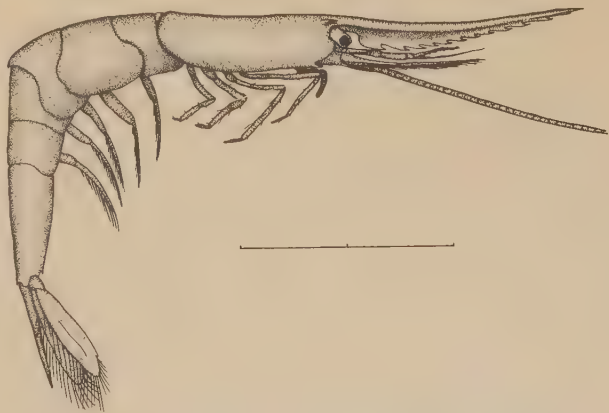


FIGURE 67.—*Tozeuma carolinense* Kingsley. Female in lateral view, 10 mm. indicated.

Habitat.—Common in beds of vegetation or similar habitats in shallow water, this species often swims in a vertical position and rests in a clinging position on blades of grass. It blends well with the background because of shape and color and is aptly named "arrow shrimp". Surface to 41 fathoms (Holthuis, 1947).

Type locality.—Fort Macon, N.C.

Known range.—Vineyard Sound, Mass., to Colon, Panama; through West Indies to Curaçao.

Remarks.—Bryce (1961) gave general ecological observations on *T. carolinense* along with a detailed study of larval development. The adults apparently feed by grazing on faunal and floral growths on marine grasses.

In North Carolina, ovigerous females are present from May to October, with one doubtful record in February. Elsewhere they have been taken in February from Bimini, March to November in Florida and Louisiana, and in December from Puerto Rico.

Bryce found that larvae hatched from ovigerous females and reared in culture dishes usually passed through eight or nine larval stages before metamorphosing into postlarvae. However, the larvae did not always transform at these stages, and, in one group reared in early fall, continued molting for an indefinite number of stages. One individual passed through 25 larval stages before the experiment was terminated. Variations in larval stages and examples of asymmetry were discussed, as were the effects of diet and temperature.

Genus *Hippolysmata* Stimpson, 1860

Stimpson, 1860, p. 26.—Holthuis, 1955, p. 115.—Hemming, 1958b, p. 156.

KEY TO SPECIES IN THE CAROLINAS

- a. Rostrum not exceeding antennular peduncles
wurdemanni (p. 84).
- aa. Rostrum greatly exceeding antennular peduncles
oplophoroides (p. 85).

Hippolysmata (Hippolysmata) wurdemanni (Gibbes)

Figure 68

Hippolyte wurdemanni Gibbes, 1850, p. 197.

Hippolysmata wurdemanni: Hay and Shore, 1918, p. 392, pl. 26, fig. 12.

Recognition characters.—Rostrum reaching distal end of second article of antennular peduncle,

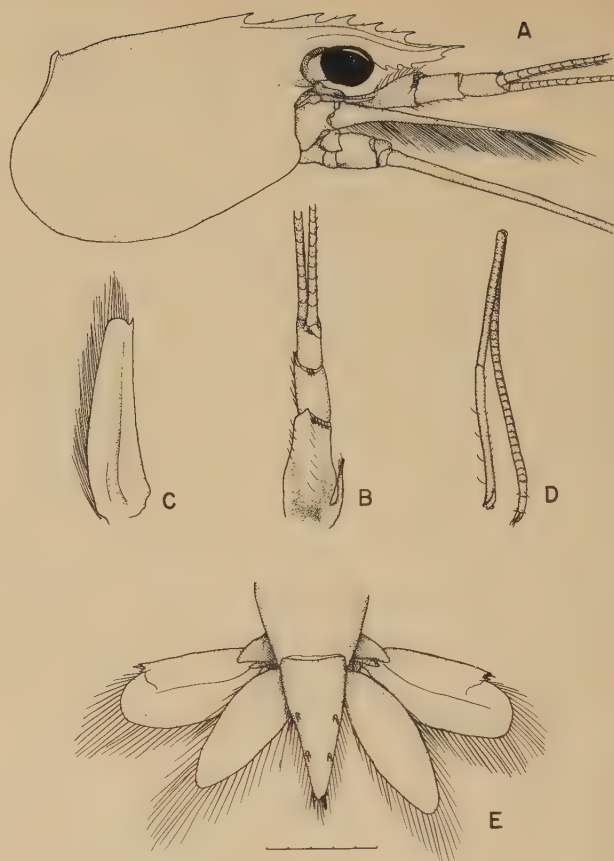


FIGURE 68.—*Hippolysmata (Hippolysmata) wurdemanni* (Gibbes). A, anterior portion of body in lateral view; B, antennule; C, antennal scale; D, second leg; E, uropods and telson in dorsal view; A-E, 5 mm. indicated.

slightly decurved, armed dorsally with four or five teeth and ventrally with three to five teeth. Carapace smooth; carinate dorsally on anterior half with a spine near base of rostrum about midway between rostral tip and posterior border; anterior margin with a strong antennal spine; anterolateral corner rounded. Eyes well developed. Basal article of antennular peduncle large, stylocerite slender, flattened, pointed, reaching a little beyond middle of article; second and third articles progressively shorter; inner flagellum slender; outer flagellum with about 20 to 30 thickened basal joints. Antennal scale long, narrow; outer margin about straight, terminating in a strong spine; lamella of scale truncate distally, about equal to spine.

Epipods on first four pairs of legs. First legs stout, about equal, reaching to end of antennal

scale; fingers about one-third length of palm, spines at tips of fingers darkened; carpus and hand of nearly equal length. Second legs much longer, slender; chela small; carpus divided into about 30 joints, last joint longest. Third to fifth legs not so slender as second; dactyls with a few coarse spines on inner border.

Abdomen smooth; posterolateral angle of fifth and sixth segments acute. Telson tapering to nearly truncate tip with a minute median projection flanked by two long, slender spines and outside these a short spine on each side; armed dorsally with two pairs of dorsal spines, anterior pair at one-third length, posterior pair at two-thirds length. Uropodal exopods with outer margin ending in two distinct teeth, between these a slender movable spine.

Measurements.—Length of body: males, 28 to 54 mm.; ovigerous females, 38 to 55 mm. (Wass, 1955, in part).

Variations.—Individuals from the northern extreme of the range differ in some respects from those in South America (Holthuis, 1959). The rostrum in South American specimens has four to seven dorsal teeth, and in specimens from the United States, four or five. Some southern specimens have stylocerites nearly as long as the basal antennular articles. In southern specimens, the tip of the lamella on the antennal scale is more truncate than in northern specimens. The second leg in Guiana material is more slender than in northern material, and the number of articulations in the carpus is higher, 33–37 as opposed to 27–31.

Color.—Translucent white with beautiful longitudinal and transverse markings of red.

Habitat.—Commonly found on stone jetties or among hydroids growing on piles or buoys; surface to 16 fathoms.

Type locality.—Key West, Fla.

Known range.—Lower Chesapeake Bay to Port Aransas, Tex.; Surinam; French Guiana; Mamanguape, São Paulo, Brazil.

Remarks.—Ovigerous females have been reported in January from Florida and in May from the Guianas (Holthuis, 1959; Wass, 1955). They have been collected in April and August from North Carolina, and in August from Louisiana.

Subgenus *Exhippolysmata* Stebbing, 1915

Stebbing, 1915, p. 94.

Hippolysmata (Exhippolysmata) oplophoroides Holthuis

Figure 69

Hippolysmata (Exhippolysmata) oplophoroides Holthuis, 1948, p. 1106.—1959, p. 112, fig. 17.

Recognition characters.—Rostrum long, slender, directed somewhat upward, reaching beyond antennal scale by nearly half of length; basal portion elevated into a crest bearing 9 to 10 closely placed teeth, one tooth some distance behind crest, remainder of upper margin with 1 to 6 widely separated teeth; ventral margin with 10 to 14 teeth. Carapace coarsely pitted; anterior margin produced into a slight lobe below eye closely followed ventrally by an antennal spine; a pterygostomian spine at anterolateral angle. Eyes well developed. Basal article of antennular peduncle with stylocerite rather broad and pointed, reaching beyond middle of article; second article somewhat longer than third; upper flagellum simple with about 20 to 25 basal joints thickened, hairy below. Antennal scale almost

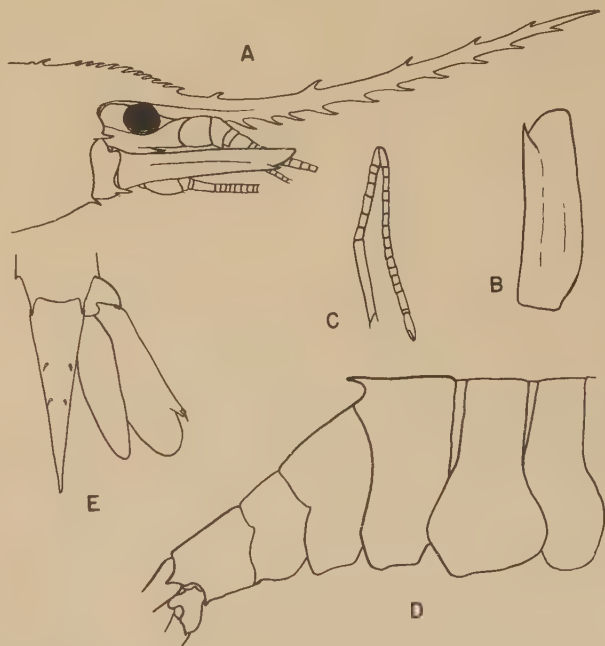


FIGURE 69.—*Hippolysmata (Exhippolysmata) oplophoroides* Holthuis. A, anterior portion of body in lateral view, $\times 3.5$; B, antennal scale, $\times 4$; C, second leg, $\times 4$; D, abdomen in lateral view, $\times 3.5$; E, telson and right uropod in dorsal view, $\times 3.5$ (after Holthuis, 1948).

three times as long as broad; outer margin slightly concave, ending in a strong tooth; lamella of scale exceeding spine; outer spine near base of scale directed ventrally.

Epipods on first four pairs of legs small but distinct. First legs equal, reaching somewhat beyond end of antennal peduncle; fingers short and blunt, immovable finger ending in a dark colored, sharp point fitting between two dark points on end of dactyl, outer surface of fingers convex, inner surface concave, fingers about five-eighths length of palm; carpus slightly shorter than chela and three-fourths length of merus. Second legs slender; slightly unequal in size, reaching almost to end of third maxilliped; chela small and slender; carpus five times length of chela and divided into 13 to 15 joints, first and last joints longest. Third to fifth legs slender; dactyls simple.

Abdomen coarsely and shallowly pitted; third segment with a dorsal carina ending in a strong, posteriorly directed spine; pleura of second to fourth segments produced posteroventrally in a narrowly rounded tip, pleura of fifth and sixth ending in a distinct sharp tooth; posterolateral angle of sixth spiniform. Telson tapering gradually to a slender point; dorsal surface with two pairs of spines, anterior pair at one-third length, second pair closer to first pair than to tip. Uropods elongate; outer margin of exopod ending in two distinct teeth, between these a slender movable spine.

Measurements.—Length of body: ovigerous females, 47 to 79 mm.

Variations.—In the case of a rostrum with one distal tooth dorsally, there were suggestions of three other small, malformed teeth.

Color.—General color pink; rostrum and anterior part of carapace pink, posterior part of carapace white and yellowish; abdomen white with pink most pronounced along posterior margins of first to fourth segments, spine on third segment almost red, fifth and sixth segments entirely pink; tail fan red, pink at base; antennular and antennal flagella pink; legs red, sometimes purplish distally; pleopods red; eggs yellow or greenish (Holthuis, 1959).

Habitat.—The species has been taken near shore, often in estuaries (15.89 ‰ over mud bottom) (Holthuis, 1959); 4 to 15 fathoms.

Type locality.—Mouth of Suriname River near Resolutie, Surinam.

Known range.—Off Cape Fear River, N.C., to Port Aransas, Tex.; British Guiana to Santos Harbor, São Paulo, Brazil.

Remarks.—Most information on this recently described species is summarized in Holthuis' (1959) account. Ovigerous females have been reported from December to July in South America and from August to October in the Carolinas. The species is more abundant than *Xiphopeneus* in British Guiana but apparently less abundant to the eastward in the other Guianas. Records from the United States are sporadic.

Family Processidae

Rostrum horizontal with dorsal surface of carapace. First pair of legs asymmetrically chelate; first leg of one side ending in a simple clawlike dactyl. Second pair of legs minutely chelate; slender; with segmented carpus.

Genus *Processa* Leach, [1815]

Holthuis, 1955, p. 116 (rev.).—Hemming, 1958b, p. 143.

Processa bermudensis (Rankin)

Figure 70

Nika bermudensis Rankin, 1900, p. 536.

Processa canaliculata: Verrill, 1922, p. 138.—Schmitt, 1935a, p. 169 (part).

Processa bermudensis: Gurney, 1936c, p. 624, figs. 44–52 (rev.).—Lebour, 1941, p. 410, figs. 28–33.—Holthuis, 1959, p. 120.

Recognition characters.—Rostrum slender, nearly straight, extending about two-thirds length of eye, bifid at end with upper process shorter than lower, a few hairs between tips. Carapace lacking antennal spine; anterior border rounded, somewhat sinuous. Eyes large, shorter than basal antennular article. Antennular peduncle with basal article excavate dorsally, longer than succeeding two articles combined, stylocerite short, somewhat truncate; second article about half again as long as third; inner flagellum filiform; outer flagellum thick, fusiform at base, slender distally, hairy, about as long as peduncle. Antennal scale about six times as long as wide; sides nearly parallel, truncate terminally; lateral spine small, slightly exceeding lamella; antenna a little longer than body. Third maxilliped with ter-



FIGURE 70.—*Processa bermudensis* (Rankin). Animal in lateral view (after Rankin, 1900).

minal article and a portion of adjacent article extending beyond antennular peduncle.

First pair of legs strong; chelate on right side; carpus a little over one-third length of merus, length about 1.5 times width; palm 1.5 times length of dactyl; left leg not chelate, carpus three times as long as wide and about two-thirds length of propodus. Second legs long, slender, unequal, chelate; carpus and merus subdivided; right leg with 18 carpal, 12 meral joints; left leg with 17 carpal, 6 meral joints; merocarpal bend of right leg reaching to or beyond end of antennal scale. Remaining legs long, slender; third shortest; fourth slightly longer than fifth; dactyls simple; propodus of fifth leg with groups of long setae, a single small spine at end and one to five additional spines along article.

Abdomen with pleura rounded. Telson three times as long as basal width; two pairs of large dorsolateral spines, first pair close to anterior end; tip subacute, armed with two pairs of stout spines, and a strong median pair of feathered setae, outer spines short, intermediate spines long. Uropods elongate; outer border of exopod ending in an acute spine flanked medially by a strong movable spine.

Measurements.—Length of body: males 14 to 16 mm.; females, 50 mm.

Variations.—The first pair of legs is usually chelate on only the right side but this asymmetry may be reversed. Relative length of the carpus of the first legs changes with age.

Color.—Larvae pale brown with glistening white chromatophores; whole body pale (Lebour, 1941).

Habitat.—Oceanic water; surface to possibly 180 fathoms.

Type locality.—Harrington Sound, Bermuda.

Known range.—Bermuda; North Carolina (restricted to recently identified material).

Remarks.—Gurney (1936c), Lebour (1941), and Holthuis (1959) have all pointed out the confusion which exists concerning identity of the species of *Processa* in the Western Atlantic. Formerly, the species found in the Western Atlantic were lumped under the name *P. canaliculata*, a name now restricted to a species in European waters (Lebour, 1936), but Lebour (1941) showed that three or perhaps four species occur at Bermuda. It is likely that more than one species occurs in the Carolinas as well.

From descriptions given by the above authors, it appears that one species occurring in the Carolinas is *P. bermudensis*, a species lacking antennal spines, although the stylocerite in North Carolina material is not shaped exactly as that shown in Gurney's illustrations. In addition, there is apparently a second species (represented by a few immature specimens in the Institute of Fisheries Research collection, all taken in night plankton tows in Bogue Sound) which has an antennal spine present, shorter legs than *P. bermudensis*, fewer joints in the carpi of the second legs than the above, and exhibits considerable variation in spination of the third and fourth legs. These specimens appear to be close to Lebour's *P. wheeleri*, but because they are so few in number and immature it is best to reserve determination until more material is available for study.

Lebour (1941) showed that *P. bermudensis* larvae are common in the plankton almost throughout the year in Bermuda, and adults were commonly found in the dredge at night, with ovigerous females occurring at least from June to October. Gurney (1936c) described eight larval stages.

Pearse (1934) too *P. "canaliculata"* from loggerhead sponges at Tortugas, Florida.

Family Pandalidae

Rostrum long and slender, laterally compressed, armed with teeth or spines. Eyes well developed. Mandibles with incisor process and a two or three-jointed palp. First pair of legs simple or microscopically chelate; second pair long, slender, chelate, carpus subdivided.

Genus *Pantomus* Milne Edwards, 1883

Rathbun, 1901, p. 117.—Hemming, 1958b, p. 159.

Pantomus parvulus Milne Edwards

Figure 71

Pantomus parvulus Milne Edwards, 1883, pl. 26, fig. 1, 1a.—Rathbun, 1901, p. 118.—Schmitt, 1935a, p. 138.

Recognition characters.—Rostrum longer than carapace, articulated with anterior margin of carapace; basal portion with three dorsal spines; lower margin with numerous slender overlapping spines; terminal half directed upward; tip bifid, lower prong longest. Carapace carinated on anterior half and armed with three spines, posterior two near together and movable, anterior spine adjoining articulation of rostrum; antennal and pterygostomian spines present. Eyes large. Antennular peduncle with basal article excavate above and longer than nearly equal second and third articles combined; stylocerite wide, broadly pointed, inner margin sinuous, tip reaching to midlength of cornea; upper flagellum about twice diameter of lower flagellum at base. Antennal scale, slender, reaching two-thirds length of rostrum, broadest near base; lateral spine exceeded by lamella.

Third maxilliped and first pair of legs reaching to tip of antennal scale. Second pair of legs longer than first; carpus subdivided; one leg with 15 to 17 carpal joints, other leg shorter, with 10 to 12 carpal joints. Third to fifth legs progressively longer than second pair.

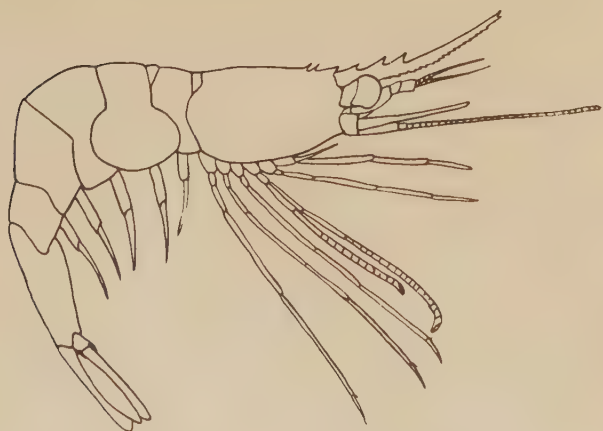


FIGURE 71.—*Pantomus parvulus* Milne Edwards. Animal in lateral view (after Milne Edwards, 1883).

Abdomen with third segment broadly carinated on posterior half; sixth segment elongate, 2.5 times length of fifth. Telson nearly as long as sixth segment, slender; sides concave, tapering to tip ending in a small, median, bulblike enlargement; two pairs of spines at tip, outer pair longest and sinuous at base, inner spines shorter, arising on terminal bulb; a row of seven or eight small dorsolateral spines on each side in distal two-thirds of length. Uropods long, narrow; exopod with lateral border ending in a slender movable spine.

Measurements.—Length of body: ovigerous female, approximately 30 mm.

Variations.—Among four of the cotypes, the rostrum varies somewhat in length and the number of carpal segments in the second legs is subject to variation.

Habitat.—Seventy-five to 248 fathoms.

Type locality.—Northern part of Yucatan Bank, lat. 23°13' N. long. 89°16' W., 84 fathoms.

Known range.—Cape Lookout, N.C., to Yucatan, Mexico; Puerto Rico; St. Croix, V.I.

Remarks.—The Catalogue of the Books, Manuscripts, Maps and Drawings in the British Museum (Natural History), vol. VI, Supplement, 1922, lists Milne Edwards' 1883 paper as follows: "The title-page (wanting to this copy), the 'Liste des Planches,' and many of the plates themselves are lithographed. Only fifty copies were issued and sent mostly to fellow workers, but a few were sold, (See letter by the Author in 'Ann. and Mag. Nat. Hist.' Vol. vi, 1890, p. 471)."

Family Crangonidae

First pair of legs subchelate, stouter than second. Second pair of legs slender, equal; carpus not subdivided; minutely chelate or simple. Rostrum small, usually dorsally flattened, not toothed.

Genus *Crangon* Fabricius, 1798

Holthuis, 1955, p. 134.—Hemming, 1958b, p. 108.

The name *Crangon* confused with the name *Alpheus* during the first half of this century, had doubtful status until nomenclatural stability was effected by the International Commission on Zoological Nomenclature (Opinion 334). The Official List of Generic Names in Zoology (Hemming,

1958b) now lists *Crangon* Fabricius, 1798, as the correct generic name for the species here considered, and the Official Index of Rejected and Invalid Generic Names in Zoology (Hemming, 1958a) lists the suppressed generic name *Crangon* Weber, 1795, and the invalid name *Crago* Lamarck, 1801, formerly applied to the species here considered.

Crangon septemspinosus Say

Figure 72

Crangon septemspinosus Say, 1818, p. 246.

Crago septemspinosus: Hay and Shore, 1918, p. 396, pl. 27, fig. 9.—Rathbun, 1929, p. 20.

Recognition characters.—Rostrum shorter than eyestalks, unarmed, tip obtuse. Carapace somewhat depressed, subcylindrical; dorsal surface with a small appressed spine back of rostrum; anterior margin with suborbital spine obtuse; antennal spine strongly produced, equaling or slightly exceeding eyes and with a minute spine below; hepatic spine well developed; anterior portion of carapace with two impressed lines, one originating in fissure in superior margin of orbit, another originating lateral to suborbital spine, both uniting above hepatic spine and disappearing posteriorly; a broad groove below and anterior to hepatic spine. Eyes moderately developed. Antennular peduncle with basal article hollowed out above, stylocerite broad, cupped longitudinally forming portion of socket for reception of eye, tip reaching nearly to end of article; second article of peduncle slightly shorter than third; inner flagellum hairy below, a little longer than antennal scale; outer flagellum shorter, smooth. Antennal scale broadest in posterior half, lamella tapering

to narrow rounded tip; lateral border slightly convex; well-developed lateral spine exceeding lamella and as long as distal width of blade. Third maxilliped reaching nearly to tip of antennule; hairy.

First pair of legs strong, subchelate; hand less than 3.5 times as long as wide, palm with a strong spine at distal end of finger; merus with a small spine on lower margin. Second pair of legs almost filiform; minutely chelate, hand hairy. Third legs stronger; fourth and fifth normal.

Abdomen, viewed dorsally, tapering from broad first and second segments to narrow sixth segment. Telson slender, tapering; with four small spines above on lateral border, first pair at two-thirds length, second midway between these and acute tip; tip flanked by three pairs of movable spines, median pair longest and stoutest. Uropodal exopods with lateral border ending in a spine flanked medially by a longer movable spine.

Measurements.—Length of body: ovigerous females from North Carolina, 25 to 60 mm. Specimens from Delaware: males, to 47 mm.; females, to 70 mm. (Price, 1962).

Color.—Ash-gray with numerous irregular, stellate, blackish-brown spots or speckled with gray, imitating the color of sand; color subject to considerable variation in shade, tail often darker (various authors).

Habitat.—Usually near bottom over sand: low-water mark to 50 fathoms, rarely to 246 fathoms.

Type locality.—"Bay shores and inlets of the sea" [east coast of United States].

Known range.—Baffin Bay to east Florida; Arctic Alaska southward to Shumagin Islands, Alaska, and Ranshima, Hokkaido, Japan.

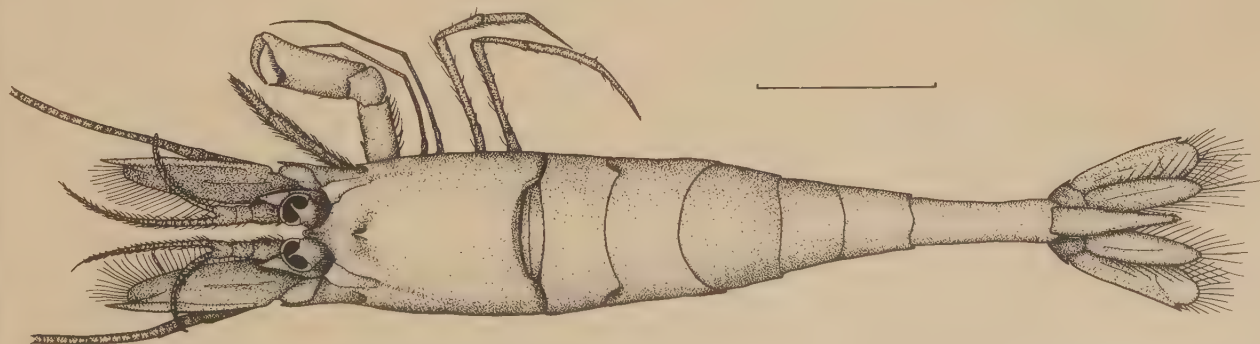


FIGURE 72.—*Crangon septemspinosus* Say. Ovigerous female in dorsal view, legs of left side not shown, 10 mm. indicated.

Remarks.—At the time of Hay and Shore's account, it was apparent that *C. septemspinosa*, with northern rather than southern affinities, fluctuates in abundance seasonally in estuaries near Beaufort, N.C. Ovigerous females have been found in North Carolina from December through May and in August and late fall (Hay and Shore, 1918, in part). Individuals taken in winter are larger than those found in spring. Juveniles have been found in this region from December to July, but from midsummer to late fall juveniles and adults disappear from estuaries.

Bigelow and Sears (1939) reported much the same pattern of occurrence in waters of the Continental Shelf from Cape Cod to Chesapeake Bay, with greatest occurrence in February dwindling to rare occurrence in July, but never abundant anywhere. They found the species limited, probably by depth and not by distance from shore, at about the 27-fathom curve, and remarked on probable importance of the species in the diet of predatory fishes. The role of the species in diets of fishes has long been recognized (Whitley, 1948).

On Georges Bank, where Whitley (1948) made all collections inside the 100-fathom curve, *C. septemspinosa* was most common in September and January, rarest in June, and usually occurred near the bottom. He reported maximum numbers in July at Woods Hole, and in August in the Bay of Fundy. Ovigerous females were found in spring and early summer. The species was judged to produce one brood a year and to have a life span of 1 year.

Price (1962), studying the biology of *C. septemspinosa* in Delaware Bay, made collections in a salinity range of 4.4 to 31.4‰ at temperature extremes of 0.0° to 26.0° C. Growth rate was estimated to be 1.6 mm. per month, with no observed seasonal variation in rate. The major breeding season was judged to be March to October, but ovigerous females were found throughout the year in salinities of 17.7 to 29.3‰, and temperatures of 0.0° to 25.0° C. First egg bearers of the year were found to be large females, with smaller ovigerous females more numerous in July. Females outnumbered the males, especially during the most active spawning season. At 21° C., eggs hatched after 6 or 7 days in the laboratory.

Contrary to the appraisal of other authors, Price judged that 3 year classes of females and 2 year classes of males occur in the shoal waters of Delaware Bay in spring. Food studies indicated a diet of planktonic crustacea and scavenged material. Sanders, Goudsmit, Mills, and Hampson (1962) found a diet of small bottom plants and animals.

Fish (1925) found the larvae appearing from February to May and as late as December at Woods Hole. Needler (1941) recorded hatching times from late spring to early summer (July) around Prince Edward Island, Canada. She described five larval stages and a postlarval stage. All these stages were obtained in July from plankton tows made about a meter below the surface along the shores of estuaries. Larvae were hatched in the laboratory, but the series of stages was worked out from plankton.

These data indicate an extended breeding season in high latitudes. Variations in seasonal abundance in different localities north of Chesapeake Bay are possibly the result in part of varied sampling methods in different years by different investigators.

Work on color control of *Crangon* and related species, too involved for appropriate summary here, has been reviewed by Kleinholz (1961).

Suborder Reptantia

Usually lobsterlike or crablike in form. Cephalothorax usually depressed. Rostrum usually small or absent, depressed if present. Antennules without stylocerite. Legs strong, first pair usually, but others never, stronger than remainder. Abdomen, whether well developed or greatly reduced, more or less depressed with first segment distinctly smaller than rest; pleopods often reduced or absent.

Section Macrura

Abdomen straight, symmetrical; usually well armored, with well-developed pleura and a strong tail fan (Schmitt, 1921).

Superfamily Scyllaridea

First article of antennule fused with epistome. Antennal scale absent. All legs nearly equal in length and none chelate except subchelate last pair in females. First abdominal segment without

pleopods; tail fan divided into a soft membranous and striated hinder part and a harder anterior portion.

Family Palinuridae

Carapace subcylindrical. Eyes not enclosed in separate orbits formed by edge of carapace. Antennae not flattened but furnished with large, long, rather rigid, multiarticulate, usually spinose flagellum.

The fossil record for the family Palinuridae extends back to the Cretaceous in North America (Rathbun, 1926, 1935).

Genus *Panulirus* White, 1847

White, 1847b, p. 69.—Hemming, 1958b, p. 174.

Panulirus argus (Latreille). Spiny lobster, crawfish

Figure 73

Panulirus argus Latreille, 1804, p. 393.

Panulirus argus: White, 1847b, p. 69.—Hay and Shore, 1918, p. 398, pl. 28, fig. 3 (rev.).—Crawford and deSmidt, 1922, p. 291, figs. 265–271.—Schmitt, 1935a, p. 172, fig. 36 (rev.).

Recognition characters.—Carapace covered with strong spines arranged more or less in regular longitudinal rows; spines above orbits very large, compressed, and curved upward and forward.

Eyes large and prominent. Antennules nearly two-thirds length of body; peduncles slightly exceeding antennal peduncle; outer flagellum shorter and thicker than inner, and strongly ciliated distally. Antennal segment with a pair of spines in front, a weaker pair about halfway to eye, a strong median spine and weaker lateral spines below insertion of antennules. Antennae very large, heavy, exceeding body by more than length of carapace; peduncles with numerous strong spines; flagellum stout, stiff, a line of cilia along inner margin and ringed with spines at intervals.

Legs rather weak, tips acute and bristly; female possessing a small subchela on fifth legs with concave opposed surfaces formed between distal portion of propodus and proximal portion of dactyl.

Abdomen smooth, each segment crossed by a furrow more or less distinctly interrupted at middle; pleural angles each produced into a strong, sharp, backwardly directed tooth deeply notched and serrated on posterior margin. Pleopods absent from first segment of abdomen; exopod of pleopods broad, laminate; endopods missing in males, females with endopods of second pleopods laminate, last three endopods bifurcated. Proxi-

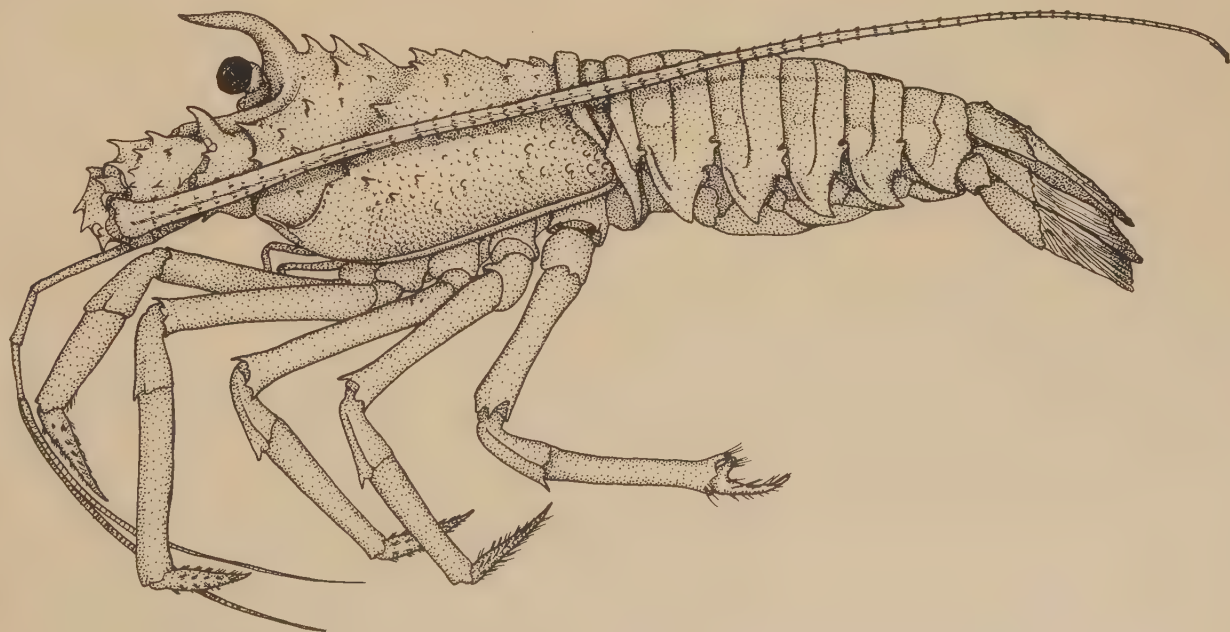


FIGURE 73.—*Panulirus argus* (Latreille). Female in lateral view, approximately $\times 0.5$.

mal division of telson with rather strong spines; distal division with weak spines and cilia in longitudinal lines. Uropods hard proximally, membranous distally; basal article bispinose, a row of denticles along margin of hard part, and lines of minute spines and setae on upper surface of membranous part.

Measurements.—Length of body from orbit to tip of telson: to approximately 450 mm. (18 inches), occasionally larger.

Variations.—Aside from individual variations which will not be discussed here, the species exhibits marked allometric variations with age as well as sexual dimorphism. These features were discussed in detail by Crawford and deSmidt (1922) and are summarized here. Antennae of the young are longer in proportion to the body than in adults. Setae present on the young disappear in the adult and the sharpness of spines on the body tends to diminish with age, except for those on anterior portions of the carapace.

As pointed out in the description, only the females have chelate fifth legs. In adult males, the second pair of legs is extraordinarily developed. They are long, rarely used in walking, and the dactyl is long, curved, and provided with a brush of setae. The length of the dactyl, its curvature and setation increase with age. Sexual differences in the pleopods are given in the description.

Males have a relatively more inflated and longer carapace than females. Conversely, in females the abdomen represents a greater proportion of total length of the body than in males. Maximum lengths of the two sexes, however, are about the same (Creaser, 1952). The posterior margin of the sternum in males is narrower than the comparable structure in females and the sternum is longer.

Color.—Coloration largely separable into two groups, (1) lightly colored individuals ranging from light gray and tan to shades of green and light brown, and (2) darkly colored individuals varying from shades of red to deep brown and blue. Abdomen spotted with yellowish ocelli; posterior margin of each segment edged with yellow or orange, lower angles of segments marked with bluish or greenish tints and sometimes additional colors. Tail fan crossed by bands of orange, yellow, and black, fringed with white. Pleopods usually orange, about half of surface covered by

a black blotch. Legs striped longitudinally with blue. Ventral surfaces of body light yellow; thoracic sternum marked with irregular radiating stripes.

Young with coloration of carapace arranged in transverse bands, usually three, middle one dark; antennae frequently ringed with alternate light and dark bands; legs ringed with blue (Crawford and deSmidt, 1922).

Habitat.—On reefs or among rocks, among growths of sponges or other objects which afford protection or places of concealment; low-tide mark to depths of about 50 fathoms. Experimentally, lobsters at Bermuda have withstood depths of 250 fathoms (Creaser and Travis, 1950).

Type locality.—Erroneously given as East Indies ("des Grandes-Indies").

Known range.—North Carolina through Gulf of Mexico and West Indies to Rio de Janeiro, Brazil; Bermuda.

Remarks.—A number of papers have been published concerning the general ecology of *Panulirus argus*. Only a summary of this work can be given here. The most comprehensive single, general treatment is that of Crawford and deSmidt (1922) for the species in Florida, but substantial additions to this work have been given by Dawson (1949, 1954), Dawson and Idyll (1951), Lewis (1951), Lewis, Moore, and Babis (1952), Marshall (1948), and Smith (1951). Mattox (1952) gave biological notes on the species in Puerto Rico, and Creaser (1950, 1952), Creaser and Travis (1950), and Sutcliffe (1952, 1953, 1957) discussed the species in Bermuda.

North Carolina must be regarded as the extreme northern edge of the range of this species, and, indeed, concentrations of the species large enough to be exploited commercially occur only in southern Florida, the West Indies southeast to Puerto Rico, and at Bermuda. A large population may exist in deep water in the northern Gulf of Mexico (Moore, 1962). Differences in growth rate and breeding habits may exist among these areas.

Panulirus argus grows to a large size. In its first year of life it reaches a length of about 2 inches (measurements of this species usually given in inches in U.S.A.) and, though growth in the young individuals is more rapid than in older animals, increments in length after that time are

about an inch a year. Adults of 16-inch length are approximately 16 years of age, the males attaining somewhat greater lengths than females.

After juvenile stages are past, molts average about $2\frac{1}{2}$ times per year, occurring most frequently from March to July and from December to February, at least in the Florida area. Among captive animals, molts without growth can occur. About 12 days elapse from the first sign of molting until the new exoskeleton is hard enough to resist denting, though hardening of the new shell is not complete until the 28th day. Travis (1954, 1955a, 1955b, 1957) gave an exhaustive study of the molting process among spiny lobsters near the age of sexual maturity. This work is beyond the scope of the present summary, but her findings show that molting among captive adolescent animals is largely confined to the warmer months at Bermuda and is more frequent than among Florida specimens. Other evidence shows that growth of the young is more rapid in Bermuda than in Florida, and that sexual maturity is reached sooner.

The mating season in Florida is principally from March through July. Sexual maturity is reached in females as small as 6 inches long, but ovigerous females under 8 inches in length are rare. Mating pairs are judged to be about the same age, and mating usually occurs in the hard-shelled stage. At the time of mating the male places a waxy spermatophore on the thoracic sternum of the female. Prior to spawning, the female scratches the surface of this packet with the chelate fifth legs. The actual egg laying is accomplished in about one-half hour, during which the female lies partially on her back forming a trough of the underside of her abdomen with the aid of the exopods of the pleopods. Eggs extruded from the oviducts pass backward from the bases of the third legs over the spermatophore and become attached to the endopods of the last three pairs of pleopods. After spawning, the spermatophore appears eroded as if enzymatic action had partially destroyed it. The eggs hatch in about 1 month. A second mating and egg laying may occur about a week after the hatch of the first batch and at this time the ovary is spent and the spermatophore almost completely eroded away. Molting of females during this season occurs only after spawning.

The spawning season in Florida is principally from March through June, and mostly in April. However, a few ovigerous females occur as late as October (December in the Bahamas). In Puerto Rico, the spawning season may be more extended than in Florida, for 22 percent of females in the commercial catch in Puerto Rico are ovigerous in September and 18 percent in October.

Direct evidence from the studies in Bermuda shows that females may lay eggs twice in a season. The number of eggs laid depends on the size of the individual, and the second brood is smaller than the first. Estimates show that a 9-inch female can lay 500,000 eggs, a 12-inch female 1,118,656, a 15-inch female 2,566,916. A second laying by a 13-inch female consisted of 1,008,788 eggs. Thus, it is estimated that a 15-inch female might lay 4 million eggs a season.

In Bermuda and elsewhere, there is apparently a movement of females from shallow to intermediate depths and from deeper water to these depths for spawning. Aside from these movements, there is evidence in Bermuda that the lobsters exhibit considerable homing tendencies, often moving as much as 5 miles against strong tides to return to the place of original capture. Adults tagged in Florida, on the other hand, have moved as much as 100 miles in 100 days (Smith, 1954), but such movement is probably exceptional.

The larva of the spiny lobster is a flattened, leaf-shaped, planktonic organism which, before its identity was known, was given the name phyllosoma. Development of the phyllosoma larvae of *P. argus* has been studied off Florida and at other points in the Atlantic Ocean from the West Indies to the southeastern coast of the United States and north of Bermuda. Bigelow and Sears (1939) found phyllosoma larvae (*P. argus*?) off Chincoteague Bay in July, 1929. Eleven stages have been described from plankton. In Florida, the bulk of freshly hatched larvae appear between June and August, the last stages being taken in December and January. The first postlarval, or puerulus, stages appear in inshore waters from January to March. Thus, larval development is judged to require 6 months, and during that time the larvae may be swept hundreds of miles from the spawning place. (Feliciano (1956) described a prenaup-

pliosoma stage which may at times be freed in the water but this has yet to be confirmed.) The puerulus is shaped like a miniature adult, but is about 17 mm. long, colorless, and has a soft exoskeleton. It is nonplanktonic and settles in shallow water. Ten postlarval stages have been distinguished. Stages one through three avoid light, but later stages show no such reactions. At the end of the first year, at the eleventh postlarval stage, the young are approximately 2 inches long.

Aside from reactions of the very young postlarvae to light, Hess (1940) showed that freshly molted adults are sensitive to light in many regions of their bodies, but as soon as the body is again sclerotized no such reactions are apparent. Sutcliffe (1956) demonstrated that in clear, shallow water lobsters sought cover in bright moonlight. He concluded that movements attributed to tidal responses were actually responses to light.

Stridulation by spiny lobsters (Palinuridae) has been described by a number of workers (Moulton, 1957) and in *P. argus* it is produced primarily by a toothed ridge medial to the bases of the antennae and extending anteriorly from beneath each eye. A corrugated membrane at the base of each antenna is played against this ridge, producing sound when the membrane is moved proximally. Two types of sound are produced, a slow rattle normally produced by animals in small groups, and a rasp which accompanies defensive behavior. A squeaking sound is also produced in an unknown manner, by vibration of the body, when a specimen is held in the hand of an observer. The effect of these sounds on other lobsters or marine life is unknown.

Pearse (1932a) determined the freezing point of *P. argus* blood at Tortugas (range -1.86° to -2.39° C.).

Family *Scyllaridae*. Spanish lobsters

Carapace depressed; exoskeleton thick, hard, sculptured or tuberculate; orbits excavated in margins of dorsal surface. Antennae short and broad with flat scalelike, stiff articles. Mandibles with a one-jointed palp. Legs simple except minutely chelate fifth pair in female.

The fossil record for the family *Scyllaridae* extends back to the lower Eocene of the Gulf Coast in North America (Rathbun, 1935).

KEY TO GENERA AND SPECIES IN THE CAROLINAS

(Adapted in part from manuscript key by
F. A. Chace, Jr.)

- a. Exognath of outer maxillipeds without a flagellum; terminal article of antennae with edge cut into deep lobes distally-----*Scyllarus* (p. 94).
- b. Prominences on carapace blunt; second article of antennular peduncles dorsally flattened; distal articles of antennae meeting, or nearly meeting, in midline; first four abdominal tergites obscurely notched posteriorly in midline; pleura of fourth abdominal segment rounded laterally.
 - c. Pregastric tooth of carapace broadly rounded; two, seldom three, distinct parallel grooves between posterior marginal groove and posterior margin of carapace; first to fourth abdominal segments with notch in posterior margin very shallow; fourth abdominal segment not elevated in midline
chacei (p. 95).
 - cc. Pregastric tooth almost always bilobed, incised; almost always a single distinct groove between posterior marginal groove and posterior margin of carapace; first to fourth abdominal segments showing a deep, narrow, median notch in posterior margin; fourth abdominal segment elevated, more or less ridgelike in midline-----*americanus* (p. 96).
- bb. One gastric and all lateral prominences on carapace sharp; second article of antennular peduncles cylindrical; distal articles of antennae not nearly meeting in midline; first four abdominal tergites deeply and acutely notched posteriorly in midline; pleura of fourth abdominal segment sharply rectangular or acute laterally-----*nearctus* (p. 97).
- aa. Exognath of outer maxillipeds with a flagellum; terminal article of antennae with edge nearly smooth or crenulate distally-----*Scyllarides nodifer* (p. 98).

Genus *Scyllarus* Fabricius, 1775

Fabricius, 1775, p. 413.

Recognition characters.—Carapace flattened, width at anterolateral corners equal to or slightly greater than length in midline; middorsal ridge and an oblique ridge on each side prominent. Antennules with first articles broad, flattened, and immovable, second article much narrower and elongate; third and fourth articles slender; flagella short; abdomen, including telson, much longer (nearly twice) than carapace; pleura of first segment incised in center of lower edge, second broad and pointed distally. Anterior pleopods of male with both rami slender, flattened, hairy on outer border; remainder with exopods small and lamellate, endopods rudimentary. Anterior pleopods of female with both rami broad and flattened; exopods of remainder lamellate,

endopods slender and with long silky hairs. Legs stout, extending beyond carapace; first legs stoutest, remainder progressively more slender; second pair longest; dactyls of first pair somewhat serrate on lower border, remainder simple; fifth legs of females subchelate. Third maxillipeds stout, basal articles prismatic.

Scyllarus chacei Holthius

Figure 74

Scyllarus americanus: Hay and Shore, 1918, p. 399, pl. 28, fig. 2.—Bouvier, 1925 (in part), pp. 448–450, pl. 7, fig. 3.—Boone, 1930, p. 84, pl. 23, fig. A. Schmitt, 1935a (in part), p. 174, fig. 39.—Holthuis, 1959, p. 126.

Scyllarus chacei Holthuis, 1960b, p. 152.

Recognition characters.—Carapace with surface squamose in part dorsally, lightly squamose below lateral borders, with feathered setae (some darkened) between squames; middorsal ridge with anterior (pregastric) eminence large, rounded, gastric eminence higher, upturned, cardiac eminence somewhat smaller than pregastric; two coalesced spines over each orbit large and somewhat separated from ridges over branchial areas. Rostrum short, rounded, sides nearly parallel. Anterior border of carapace emarginate. Orbits deeply excavated with a broad anterior notch, a blunt tooth on proximal (fixed) antennal article in center of notch. Anterolateral corners of carapace spiniform, lateral borders roughened with squames; a rather deep notch behind orbit and another one farther back; area between posterior marginal groove and posterior margin of carapace nearly smooth but traversed by two, seldom three, distinct parallel grooves.

Second antennular article elongate, flattened above, anterior margin obliquely truncate. Antennae spatulate, somewhat punctate; distal article with irregularly rounded anterior border cut into seven elongate, somewhat separated, lobes with rounded ends, edges ciliated; medial two lobes shortest and sharpest, lateral lobe obliquely truncate and broadest; penultimate article short, bilobed in dorsal view; proximal movable article cordate, a prominent ridge throughout length to spiniform tip, a less conspicuous and irregularly shaped medial ridge, edges spinose.

Second, third, and fourth abdominal tergites (and to some extent first) with arborescent furrows running inward and forward toward midline; first to fourth segments with median notch in posterior margin very shallow, fourth segment



FIGURE 74.—*Scyllarus chacei* Holthuis. Male in dorsal view, approximately $\times 2$. Bob Simpson photo.

not elevated in midline. Third to fifth pleura rounded distally, sixth with a rounded anterolateral lobe. Sternum triangular, broad at base, smooth with furrows ciliated; male with slight midventral elevation on fifth plate, elevation less evident in female.

Measurements.—Length of carapace, 19 mm.; length of abdomen 35 mm.

Habitat.—Nine to 100 fathoms.

Type locality.—North-northwest mouth of Marowijne River, about 20 miles off coast of Surinam.

Known range.—Off Cape Lookout, N.C., through Gulf of Mexico, West Indies, and Caribbean Sea to off Cape São Roque, Brazil.

Remarks.—Ovigerous females have been taken off Florida in March, South Carolina in July, Surinam in August and September, and northeast Brazil in November.

Scyllarus americanus (Smith)

Figure 75

Arctus americanus Smith, 1869b, p. 119.

Scyllarus americanus: Bouvier, 1925 (in part), pp. 448–450.—Holthuis, 1960b, p. 152 (restr.).

Recognition characters.—Carapace with surface squamose in part dorsally, a little squamose below lateral borders posteriorly, lightly tuberculate toward epistome, with feathered setae (some darkened) between squames; middorsal ridge with anterior (pregastric) eminence large, bilobed anteriorly, gastric eminence sharper and more elevated, cardiac eminence not so sharp, bi-



FIGURE 75.—*Scyllarus americanus* (Smith). Ovigerous female in dorsal view, approximately $\times 1.5$. Bob Simpson photo.

lobed; two coalesced blunt spines over each orbit large and somewhat separated from ridges over branchial areas. Rostrum short, rounded at tip, a blunt keellike middorsal tubercle above. Anterior border of carapace emarginate. Orbits deeply excavated, margins broad, with a broad anterior notch; a blunt tooth on proximal (fixed) antennal article in center of notch. Anterolateral corners of carapace spiniform, lateral borders roughened with squames; a rather deep notch behind orbit and another one farther back. Area between posterior marginal groove and posterior margin of carapace faintly squamose and traversed almost always by a single distinct groove.

Second antennular article elongate, flattened above, anterior margin obliquely truncate. Antennae spatulate, somewhat punctate, surface variably covered with feathered setae; distal article with irregularly rounded anterior border cut into six somewhat separated lobes, edges ciliated, medial lobe short, spiniform, next much larger and less pointed, following three about equal in length, tips rounded, lateral lobe about twice width of intermediate lobes; penultimate article short, bilobed in dorsal view; proximal movable article triangular in outline, edges spinose, two lateral spines larger than four variably sized medial spines, a prominent ridge running to apical spine nearly dividing article in half.

Second, third, and fourth tergites of abdomen (and to some extent first) with arborescent furrows running inward and forward toward midline. First to fourth segments with median notch in posterior margin fairly deep and narrow; fourth segment elevated, more or less ridgelike in midline. Third to fifth pleura rounded distally, sixth with a narrowly rounded anterolateral lobe. Sternum triangular, broad at base; smooth with furrows ciliated; male with a low tubercle in center of fifth sternite, female similar.

Measurements.—Ovigerous female: length of carapace, 25 mm., width, 29 mm.; length of abdomen, 45 mm.

Habitat.—Surface to 19 fathoms, usually 3 to 12 fathoms.

Type locality.—Edgmont Key, Fla.

Known range.—Off Bogue Inlet, N.C., to southern Florida; Campeche Banks off Mexico.

Remarks.—Ovigerous females have been taken in southern Florida in September.

Scyllarus nearctus Holthuis, 1960b, p. 151.*Scyllarus arctus paradoxus*: Rathbun, 1900b (in part), p. 309.

Recognition characters.—Carapace with surface squamose in part dorsally, but only on or near ridges and sides, smooth below except a sinuous submarginal row of tubercles and a lightly granulate area posteriorly, densely ciliate above between squames and on smooth areas. Rostrum short and acute; pregastric tooth above it about same size, gastric tooth larger, acute, all three of these directed forward. Cardiac eminence blunt, bilobed at apex. Gastric tooth and cardiac eminence with squames at base, rostrum and pregastric tooth in smooth area. Lateral ridges ending anteriorly in a forwardly directed spine. Front emarginate with a small projection about halfway between rostrum and orbit. Orbits deeply excavated, upper border composed of two spines coalesced at base, lower border an inflated ridge more or less interrupted by two subequal spines at anterolateral corner; anterior notch partially occupied in middle by a large serrulate tooth on first (fused) antennular article and another eminence forming articulation of second antennal article. Anterolateral corners of carapace drawn out to a strong spine, lateral border with a notch behind eye and another less definite notch behind anterior end of branchial ridge. Posterior margin of carapace with a sharp but broadly opened notch in midline; area between posterior marginal groove and posterior margin of carapace traversed by two rows of squames.

Anterior border of first antennular article with low teeth or irregularities; second article cylindrical with a flattened, rounded distal projection; succeeding articles slender, flagella short. Antennae spatulate, fairly smooth, ciliated, edges densely covered with longer feathered setae; distal article semielliptical in outline, edge broken into six well-separated lobes with narrowly rounded tips, inner lobe smallest, outer broadest and subtruncate, a suggestion of a seventh lobe medially; penultimate article short, irregularly spined and lobed; first movable article roughly triangular with apex formed by a strong spine, two spines on outer border and three spines on inner border, apical spine and first two inner spines with small spurs on medial borders, third spine at medio-

posterior border smaller, a definite ridge running across article from articulation to apex.

Second to fifth abdominal segments (and to some extent first) with arborescent furrows running inward and forward toward midline. First to fourth segments with median notch in posterior margin deep and narrow. Third and fourth with distal edge of pleura rounded anteroventrally, angled at posteroventral corner; fifth broadly rounded distally; sixth with anteroventral lobe broad and rounded. Telson with four flattened spines at distal edge of hard portion. Each ramus of uropods with a spine at same level on outer margin.



FIGURE 76.—*Scyllarus nearctus* Holthuis. Male paratype in dorsal view, approximately $\times 1.5$. Bob Simpson photo.

Sternum triangular, narrower in males than in females, smooth, a little pubescent in grooves. Male with a strong, shelflike protuberance on sternite between last pair of legs, and with a strong sharply ridged shoulder extending over genital pore. Female with a low eminence on sternite between last pair of legs.

Measurements.—Ovigerous female: length of carapace, 24 mm., width, 26 mm.; abdomen, length, approximately 50 mm.

Habitat.—Thirty to 100 fathoms.

Type locality.—South of Dry Tortugas, Fla.

Known range.—Off Cape Hatteras, N.C., through Gulf of Mexico and West Indies to State of São Paulo, Brazil.

Remarks.—Ovigerous females have been taken off North Carolina in June.

Genus *Scyllarides* Gill, 1898

Gill, 1898, p. 99.—Verrill, 1922, p. 18. (rev.).—Hemming, 1958b, p. 94.

Scyllarides nodifer (Stimpson)

Figure 77

Scyllarus nodifer Stimpson, 1866, p. 48.—Stimpson, 1871b, p. 123.

Scyllarides americanus Verrill, 1922, p. 24, pls. 5–6.

Scyllarides nodifer: Holthuis, 1960b, p. 153.

Recognition characters.—Carapace longer than wide, subtruncate in front, coarsely and unevenly granulate, granules elevated, not crowded, each surrounded by more or less complete circle of stiff hairs; anterolateral corners forming nearly a right angle terminating in an obtuse tooth; cervical notch and groove well marked with numerous denticles on margin in front of and behind notch; posterior transverse groove deep and conspicuous; gastric area with a large, broad-based, prominent median ridge divided into a smaller anterior and larger posterior part, each portion ending in an anterior, large, conical, obtuse or bilobed tubercle with other similar but smaller tubercles and coarse granules around and behind apex; cardiac region with a prominent but less elevated area with larger tubercles than on adjacent surface; a similar ridge on each branchial area. Orbits large, with prominent, thick borders, anterior notch wide and deep.

Antennae with distal article broader than long, edges broadly and evenly rounded, minutely lobulate and crenulate, fringed with short, close hairs; exposed portion forming a half oval, upper

side covered with small, rough granules and small pits bearing tufts of short hairs in large adults, smoother in small individuals. Penultimate movable article showing two lobes beneath. Second movable article distinctly wider than long, broader than distal article; distal lobe terminating in nearly right angled point in large adults, armed with a spine in smaller specimens; edges dentate with many small teeth and some larger ones, a larger stout tooth near inner curve of inner margin; inner lateral lobe stout, thick, enlarged toward end; inner edges of these lobes of both antennae separated by a space about equal to orbit of eye. First movable article irregularly four-lobed above; small outer lateral lobe with about three denticles; median or distal lobe swollen and coarsely granular; inner lobe obliquely oblong with inner edge truncate and denticulate; prefrontal or rostral lobe a little broader than long, widest distally, swollen laterally, with concave sides and a median groove.

Outer maxillipeds large, basal articles stout. Legs projecting beyond carapace; first pair stouter than others, propodus considerably swollen, dactyl stout; fifth pair with propodus most slender; merus and carpus of all pairs, except carpus of first, with a finely serrulate carina ending in a sharp distal tooth; carpi, except first, with a lateral carina ending in a distal tooth; meri of last four legs with a ventrolateral carina ending in a sharp spine distally (carina sharpest on legs three and four) and each with a blunter medial spine distally.

Underside of bases of legs and sternum roughly sculptured, one larger acute or pyramidal elevation on sternum opposite base of each leg.

Abdomen strongly sculptured, elevated areas coarsely granulated and hairy, much like carapace. Second to fourth segments with a median, elevated, obtuse ridge, covered with large granules; fifth segment with slight ridge. Pleura large, angular; that of second segment largest, subacute, both edges with dentations about as large as adjacent granules; those of third to sixth segments more minutely dentate on posterior border, nearly smooth or minutely crenulate on anterior border. Telson broader than long, subtruncate distally; posterolateral angles broadly rounded; granulated and hairy proximally, covered with numerous forked ridges and grooves



FIGURE 77.—*Scyllarides nodifer* (Stimpson). Female in dorsal view, approximately $\times 0.5$. Bob Simpson photo.

distally becoming fine near edge. Uropods broad, sculptured as telson. Sternum of second segment in males bearing a sharply raised, serrate, heavily sclerotized ridge.

Measurements.—Length of carapace: female, 127 mm. Larger specimens have been observed but not measured.

Variations.—Smaller specimens are smoother than adults.

Color.—Body covered with irregular small brown spots on a grayish brown to yellowish background; many orange-red tubercles on edges, across ridge near rear edge of carapace, base and edges of antennal lobes; darker red spots at sides of gastric region, on anterior lobes of carapace and at middle of first abdominal segment; underparts yellow with darker yellow and brown spots; legs banded with red and purple; flagella of antennules purple.

Habitat.—Mud, shell, coral, and sandy bottoms; 16 to 40 fathoms.

Type locality.—Florida Keys.

Known range.—Bermuda; Cape Lookout, N.C., to Cuba; off Pensacola, Fla.

Remarks.—Little is known of these lobsters. They are sometimes used for food or bait.

Superfamily **Thalassinidea**

Exoskeleton often more or less membranous. Carapace compressed. Last articles of second to fourth legs not curved and flattened. Abdomen large, symmetrical, extended, sometimes with well-developed pleura; appendages of sixth segment usually adapted for swimming.

Family **Callianassidae**

Body shrimplike. Carapace with a "*linea thalassinica*." Antennal peduncle five-jointed;

antennal scale vestigial, no antennal acicle. First pair of legs unequal or subequal, perfectly or imperfectly chelate; third and fourth pairs simple; others variable. Abdomen extended; pleura small or absent; sixth abdominal appendages with no sutures; tail fan well developed; broad appendages on third to sixth abdominal segments (after Hay and Shore, 1918; Schmitt, 1921).

KEY TO GENERA AND SPECIES IN THE CAROLINAS

- a. Rostrum small; first two pairs of pleopods different from following three pairs; chelipeds dissimilar and unequal.....*Callianassa* (p. 100).
- b. Uropodal endopods narrow, about 4 times longer than broad.....*C. major* (p. 100).
- bb. Uropodal endopods not much longer than broad.....*C. atlantica* (p. 102).
- aa. Rostrum large; second pair of pleopods like following three pairs; chelipeds alike and subequal.....*Upogebia affinis* (p. 103).

Genus *Callianassa* [Leach, 1814]

Leach, [1814], p. 400.—Hemming, 1958b, p. 142.

The genus *Callianassa* has a fossil record extending back to the Jurassic (Rathbun, 1926).

Subgenus *Callichirus* Stimpson, 1866

Stimpson, 1866, p. 47.

Callianassa (*Callichirus*) *major* Say

Figure 78

Callianassa major Say, 1818, p. 238.—Schmitt, 1935b (rev.).
Callichirus major: Hay and Shore, 1918, p. 407, pl. 29, fig. 10.—de Man, 1928, p. 30 (rev.).

Recognition characters.—Integument more or less thin and membranous; chelipeds and an oval plate covering anterior three-fourths of carapace, being most hardened portions. Rostrum minute, somewhat obtuse; a similar projecting lobe at each side on margin of front. Cornea of eyes minute, situated at about middle of outer margin of flattened and pointed ocular peduncles. Antennular peduncles about two-thirds as long as carapace, stout, densely hairy below; each with two flagella about as long as distal article of peduncle. Antenna slender, longer than carapace, peduncle bent between second and third article.

Chelipeds unequal, showing sexual dimorphism. Males with major cheliped rather large; granular along proximal lower edge of carpus, lower edge of merus and over entire ischium; propodus and carpus about equal in length, twice as broad as merus and more than three times as broad as

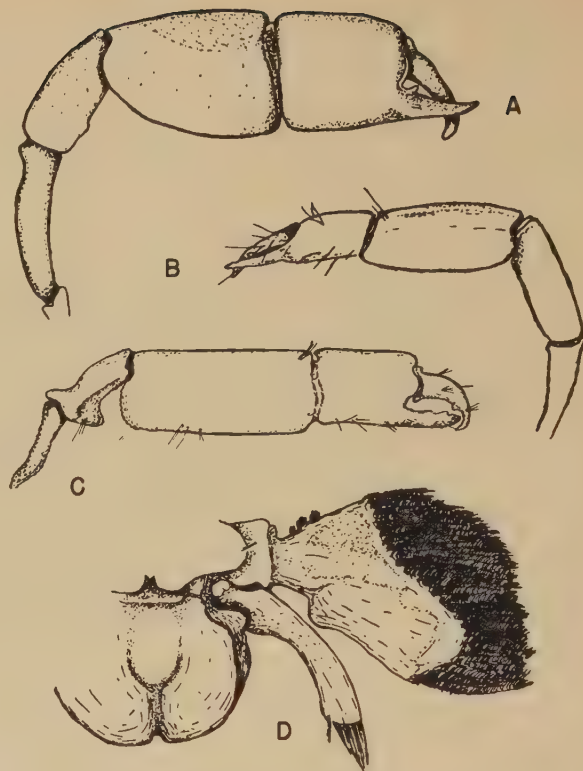


FIGURE 78.—*Callianassa* (*Callichirus*) *major* Say. A, major cheliped of female, approximately $\times 2$; B, minor cheliped of male, approximately $\times 2$; C, major cheliped of male, approximately life size; D, right uropod and portion of telson in dorsal view, approximately $\times 3$ (after Lunz, 1937b).

ischium; merus with a strong tooth on lower proximal border; fingers strong, dactyl hooking over outside fixed finger, a strong tooth near base. Major cheliped of female weaker, not granular; propodus and carpus proportionately shorter than in male; merus without tooth on lower proximal border; dactyl hooking over inside fixed finger. Minor cheliped of male and female similar, small; fingers weak, meeting only at tips; carpus as long as hand and somewhat wider. Chelipeds and first three pairs of walking legs much compressed; margins of distal articles on first two pairs especially sharp; first walking legs chelate, with long cilia on lower margin; second legs with propodus transverse, it and small triangular dactyl densely ciliate; third and fourth walking legs with last two articles hairy, last legs subcylindrical.

Abdomen long, gradually widening from anterior end to third segment, then narrowing

slightly to sixth; sixth segment deeply grooved above. First two pleopods small and slender in male, larger and definitely biramous in female; remaining pleopods broad and overlapping. Uropods with exopod broad, rounded distally; distal half covered with mat of dense short hair becoming longer on border; endopod narrow, obliquely truncate, hairy at tip only. Telson with an inflated area on each side giving notched or fissured appearance.

Measurements.—Length of body: males, 95 mm.; females, 92 mm.; ovigerous females, 80 mm. (Lunz, 1937b).

Color.—Transparent gray except for porcelain white chelipeds and hardened portion of carapace (Lunz, 1937b).

Habitat.—Burrows in sandy shores on or near open ocean; intertidal zone to 1 fathom.

Type locality.—Coasts of Southern States and east Florida [St. Johns River].

Known range.—Beaufort Inlet, N.C., to eastern Florida; Grand Terre Island to Timbalier Island, La.

Remarks.—For many years this species was known only from a single specimen from Beaufort, N.C., and early descriptions of specimens from South Carolina and Florida. The rarity of occurrence in collections is due to the secretive burrowing habits of the form, for it easily escapes detection of the casual observer using conventional methods of collection. (Collections can be made by removing the mouth of the burrow, dropping pebbles or debris down the hole, waiting for the animal to appear at the exposed surface, then jabbing a shovel into the sand below the animal, thus cutting off escape into the burrow.) Such habits no doubt also enhance chances for fossilization, for the genus is abundant in the Cretaceous and Eocene of the Gulf coastal plain, and somewhat less abundant in later deposits down to the present time (Rathbun, 1935).

Lunz (1937b) was the first recent student to determine the habitat and abundance of the species in South Carolina and his studies were closely followed by those of Willis (1942) in Louisiana, and Pearse, Humm, and Wharton (1942), and Pohl (1946) in North Carolina.

The animal lives in deep burrows on sandy beaches that either face the open ocean or are close to it. In Louisiana, the burrows occupy a

band from the intertidal zone to a distance of over 100 feet from shore in 5 to 6 feet of water. The tubular burrows, usually vertical to the surface, are divided into three portions. The mouth, about 5 mm. in diameter, opens into the upper portion, 5 to 20 cm. long and 5 to 8 mm. in diameter. From this the middle portion, 10 to 15 cm. long and often angled, widens gradually to approximately 20 mm. The third portion, 20 mm. wide, is the longest. An approximate average depth of the whole burrow is 146 cm. with variations from 60 to over 210 cm. Branches are common and arise most often from the middle portion. Characteristically, the burrows are lined with a brown material, thinnest in the upper portion and thickest (3 to 7 mm.) in the lower portion. The burrows often end in an enlarged pocket lined with crushed shell, and in some the lined tube extends below the pocket.

Burrow mouths are often surrounded by fecal pellets of *C. major*, which resist rapid disintegration in water. On some South Carolina beaches, such pellets were washed together in patches measuring up to 10 by 50 feet and piled to a depth of 0.25 inch. Mouths of burrows are not uniformly scattered but tend to be clumped in patches or tracts, often as dense as three or four openings per square foot. Chimneylike structures at the mouths of burrows noted by Say have not been confirmed, but a small raised ridge of sand often surrounds burrow mouths. Other mouths are not marked or may be located in a depression.

In captivity, the animals burrow in sand headfirst with the anterior appendages until a shallow pit is constructed, then the animals reverse themselves and continue to burrow tailfirst. Though the shrimp do at times emerge voluntarily from their burrows, such behavior is probably infrequent and may be confined to the breeding season (Lunz, 1937b). The species is well fitted for a fossorial life by virtue of the slender, elongate body, thin exoskeleton, and flattened hairy appendages adapted for burrowing, carrying sand, sifting food, and pumping water for feeding and respiratory currents. Examination of gut contents has shown an amorphous mass containing sand grains, diatoms and other algae, and many bacteria.

Ovigerous females have been reported from South Carolina in July and August, and they are

known from North Carolina in June and July. Pohl (1946) counted 8,170 attached eggs on one female. *Pinnixa cristata* has been found as a commensal in the burrows.

***Callianassa (Callichirus) atlantica* Rathbun**

Figure 79

Callianassa stimpsoni Smith, 1873c, p. 549, pl. 2, fig. 8.—Hay and Shore, 1918, p. 406, pl. 29, fig. 5.

Callianassa atlantica Rathbun, 1926, p. 107.—de Man, 1928, p. 37 (rev.).—Rathbun, 1935, p. 104.—Schmitt, 1935b, p. 4.

Recognition characters.—Integument smooth, shining, thin, almost membranous. Carapace about one-third length of abdomen, thin but with oval thickened plate on gastric region. Rostrum small, acute, flanked by a small triangular prominence at each side on frontal margin. Eystalks small, flat, contiguous medially; pointed tips slender, curved outward and upward; cornea small, situated on outer border. Antennular peduncles about one-half length of carapace; flagella about as long as distal article of peduncle, densely hairy below. Antenna slender, longer than carapace; peduncle much shorter than that of antennules, bent between second and third articles. Third maxilliped operculiform; dactyl slender.

Chelipeds unequal, showing sexual dimorphism. Larger cheliped of male with fingers about equal in length, hairy, tips incurved; cutting edge of dactyl with a long, low, truncate tooth at base, smaller teeth distally; immovable finger with small teeth; palm hairy below, upper border ridged along proximal two-thirds; carpus as wide as but shorter than palm, upper and lower border ridged; merus articulating with carpus by extreme upper angle, a prominent, denticulate tooth on lower border proximally; ischium with six or seven subacute teeth on lower border. Smaller cheliped of male with fingers a little longer than palm; carpus four times as long as broad distally, a little longer than palm, half again as long as merus; merus twice as broad as long. Larger cheliped of female less toothed than in male; smaller cheliped as in male.

Abdomen with third to fifth segments of about equal width, each with a small patch of fine hairs on posterolateral angle; sixth segment broader than long. Male with no pleopods on first and second segments. Female with uniramous pleopods on first segment; slender, biramous pleopods on second segment; remainder well developed in

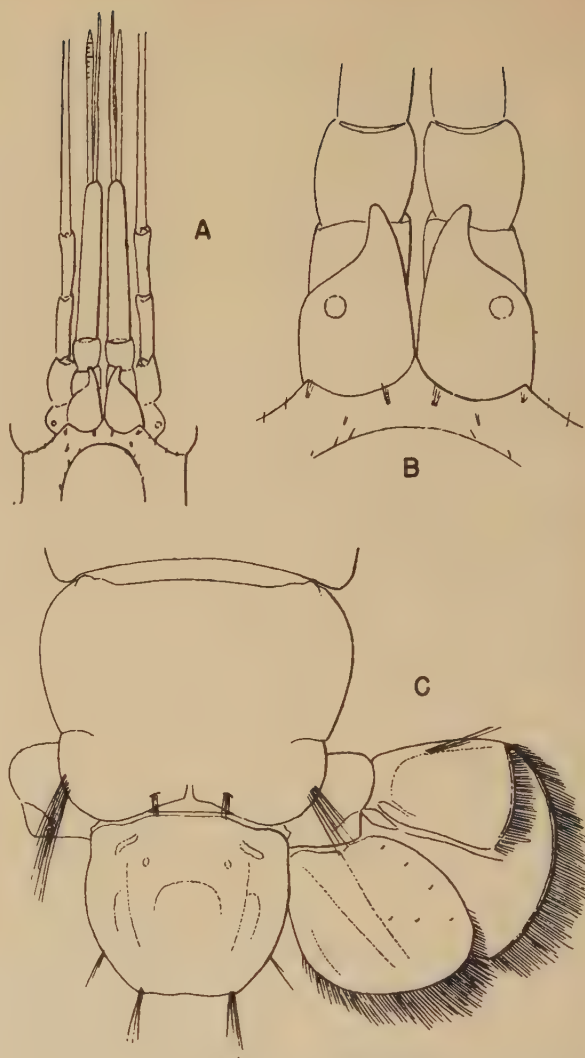


FIGURE 79.—*Callianassa (Callichirus) atlantica* Rathbun. A, frontal region in dorsal view; B, frontal region, eyestalks and antennules in dorsal view; C, sixth abdominal segment, right uropod and telson in dorsal view (after de Man, 1928).

both sexes. Telson nearly as long as broad; subtruncate distally, corners rounded. Exopods of uropods broader than endopods, both rami densely fringed with hairs distally.

Measurements.—Length of body: male, 59 mm.; female, 68 mm.

Habitat.—Muddy shores and bottoms in shallow water (Sumner, Osburn, and Cole, 1913a, b); shoreline to approximately 21 fathoms.

Type locality.—"Our species ranges from the coast of the Southern [United] States north to Long Island Sound" (Smith, 1873c).

Known range.—Bass River, Nova Scotia, to South Carolina; Franklin County, Fla.

Remarks.—Both de Man (1928) and Schmitt (1935b) pointed out that Rathbun renamed this species because the name *stimpsoni* was preoccupied by a fossil species of *Callianassa* named by Gabb in 1864. *Callianassa atlantica* itself has a fossil record extending from a first appearance in the upper Miocene of North Carolina and Virginia, and a later occurrence in the Pleistocene of Maryland to the present (Rathbun, 1935).

Ovigerous females have been taken in Massachusetts and South Carolina in July. Juveniles 4 mm. long have been collected on the surface in September in Massachusetts (de Man, 1928). This form is rarely taken in the Carolinas but has been collected in areas ranging from salty estuaries to offshore fishing banks.

Genus *Upogebia* [Leach, 1814]

Leach, [1814], p. 400.—Hemming, 1958b, p. 143.

Upogebia affinis (Say)

Figure 80

Gebia affinis Say, 1818, p. 241.

Upogebia affinis: Hay and Shore, 1918, p. 408, pl. 29, fig. 9.—Schmitt, 1935a, p. 196 (rev.).

Recognition characters.—Integument, except dorsal part of carapace and of legs, more or less membranous. Carapace about half as long as abdomen; cephalic portion about twice as long as thoracic, nearly flat above, anteriorly rugose and covered with short, rigid hairs. Rostrum large, flanked on each side at base by a large spine, spiny beneath in midline. A small upcurved spine behind eye on anterior margin, and a minute lateral spine behind cervical groove. Eyestalks concealed, pubescent above; corneal surface small. Antenna a little less than twice as long as carapace.

Chelipeds stout, a fringe of long hairs below; hands with an external, dentate ridge above, a median row of acute spines and an internal line of stiff hairs; immovable finger curved, movable finger much longer, denticulate above at base, cutting edges of both toothed near base; carpus grooved on outer face with a row of small spines and a strong marginal spine below, a row of small teeth on inner margin, and six acute spines along distal margin above; merus with a small spine above and a row of spines beneath. First pair of

walking legs hairy at tips and along lower margin; merus with a strong spine at base. Remaining legs hairy at tips.

Abdomen gradually increasing in width from first to fourth segment, fifth narrower posteriorly, sixth subquadrate; lateral portions of third and fourth segments densely pubescent and all with pleura marked off by an impressed line. Tail fan densely hairy distally. Uropodal endopods truncate and with a median rib and costate outer border; exopods rounded distally and with two ridges. Telson broad, subquadrate, with an impressed median line.

Measurements.—Length of body: males, 61 mm.; females, 63 mm.

Variations.—Schmitt (1935b) mentioned the variability in spination of the lower border of the rostrum and multiple spination or lack of spines behind the cervical groove. Young specimens often lack these spines.

Color.—Gray, blue, or yellowish gray dorsally, tinged with light blue medially on tail fan and on fifth segment of abdomen, interlaced with uniform light lines; an oblique blue spot on side of

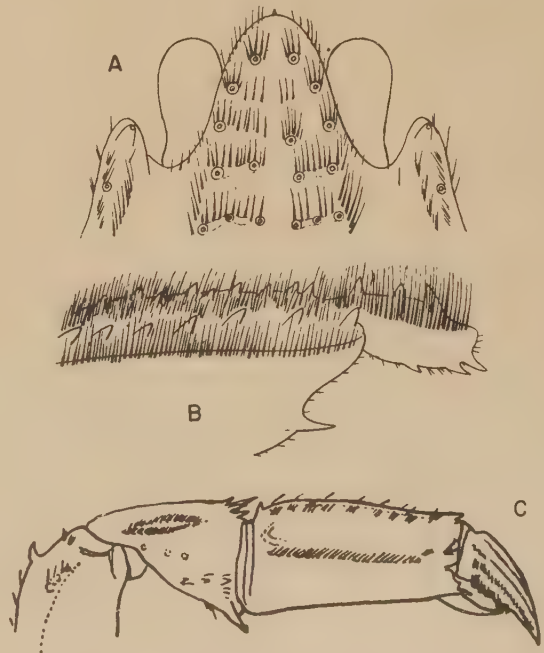


FIGURE 80.—*Upogebia affinis* (Say). A, rostral region and eyes of semiadult female in dorsal view; B, rostral region of semiadult female in lateral view; C, major chela (after de Man, 1927).

carapace at base of antenna extending postero-dorsally; underparts light (various authors).

Habitat.—Burrows on estuarine mud flats and in shallow estuaries; intertidal to 15 fathoms.

Type locality.—Georgia.

Known range.—Wellfleet, Mass., to Rockport, Tex. (Hedgpeth, 1950); through West Indies to Maceió, Alagoas, Brazil (de Man, 1927).

Remarks.—A species of *Upogebia* is known from the Eocene of Alabama (Rathbun, 1935).

Ecological notes on *U. affinis* in North Carolina were reported by Pearse (1945). The species inhabits muddy situations in estuaries where salinities are fairly high. Its burrowing habits are similar to those of *Callianassa*. Wass (1955) found burrows prevalent in Florida where the marine grass *Halodule wrightii* stabilizes muddy substrates. Burrows examined by Pearse were 30 to 50 cm. deep with openings about 30 cm. above low-tide mark. They were often branched, containing several individuals each in its own branch, and showed one to eight small openings at the surface. In communal burrows he often found two or three ovigerous females and one or two juveniles. Like the burrows of *Callianassa*, those of *U. affinis* are narrowest in the upper portion. Pearse concluded that the animals seldom leave their confines.

In captivity, *U. affinis* made only feeble attempts to burrow. In nature, however, the animals are active and pump water vigorously from the anterior to posterior end of the body by flapping movements of the pleopods. Food is apparently strained from the water by the hairy mouth parts and walking legs, and probably consists largely of organic materials swept in the water current.

Ovigerous females were studied in detail in August, though Hay and Shore (1918) pointed out that the breeding season lasts throughout the summer, and juveniles have been collected in Bogue Sound, N.C., in plankton tows from early April to late October. Fish (1925) reported larvae at Woods Hole from mid-July to the latter part of October, but they were most abundant in early August. A single female may produce about 10,000 eggs at a time. They are borne on the first four pairs of pleopods. In captivity, more zoeae were hatched at night than in daytime. Pearse cited MacGinitie (1934) for evidence that *U. affinis*, like members of the related genus *Callianassa*,

may live several years, though there is no evidence supporting this idea for the former.

Upogebia affinis is commonly parasitized in North Carolina by the bopyrid, *Pseudodione upogebiae* Hay. Pearse (1952a) described a parasitic isopod, *Phyllodurus robustus*, from a Florida specimen.

Section *Anomura*

Abdomen well developed, either symmetrical and flexed beneath thorax, exceptionally extended in a straight line usually flexed on itself, or asymmetrical, coiled and imperfectly armored, almost always with biramous appendages on sixth segment. Carapace usually depressed, free from epistome, traversed on either side in longitudinal or obliquely longitudinal direction by distinct suture (*linea anomurica*) more or less marking off side-wall of carapace from dorsal and dorsolateral portion. Last thoracic sternum free (or atrophied). First pair of legs well developed and chelate; second and third pairs well developed, not chelate; fifth pair markedly different from third.

Superfamily *Galatheidea*

Carapace more or less depressed. Abdomen relatively well developed, not closely folded beneath cephalothorax, symmetrical, and with well-developed pleura, but to some extent not capable of complete extension. Eye scales absent. Antennal peduncle with third article indistinct. Last thoracic sternum distinct. Second to fourth legs with dactyl not curved and flattened. Males with at least a pair of sexual appendages.

Family *Galatheidae*

Carapace longer than wide, often ornamented with transverse, ciliated lines. Rostrum distinct and strongly pointed, projecting beyond eyes. Antennular peduncle elongate. Antennae with four-jointed peduncle. Chelipeds greatly elongated, slender. First, second, and third walking legs well developed; fourth leg feeble, reduced in size. Abdomen bent upon itself but not folded under thorax; males with a pair of sexually modified pleopods on segment two, a pair of uniramous pleopods on segments three, four, and five; females with rudimentary pleopods on second abdominal segment, fully developed pleopods on three, four, and five.

KEY TO GENERA AND SPECIES IN THE CAROLINAS

a. Rostrum rather broad, margins toothed

Galathea rostrata (p. 105).

aa. Rostrum slender, toothless except for supraocular teeth at extreme base-----*Munida irrasa* (p. 105).

Genus *Galathea* Fabricius, 1793

Fabricius, 1793, p. 471.—Milne Edwards and Bouvier, 1897, p. 13.—Hemming, 1958b, p. 143.

Galathea rostrata Milne Edwards

Figure 81

Galathea rostrata Milne Edwards, 1880, p. 47.—Hay and Shore, 1918, p. 402, pl. 29, fig. 4 (rev.).—Chace, 1942, p. 30.

Recognition characters.—Carapace somewhat flattened; transverse ciliated ridges prominent, at least four continuous for entire width of carapace; lateral margins with a number of acute spines. Front prolonged into a broad, acute rostrum armed with four strong, anteriorly pointing spines on each side. Third maxilliped with inner margin of merus armed with three or four spines.

Chelipeds nearly twice as long as body, comparatively heavy; with rows of spines or spiniform granules along margins and appressed,

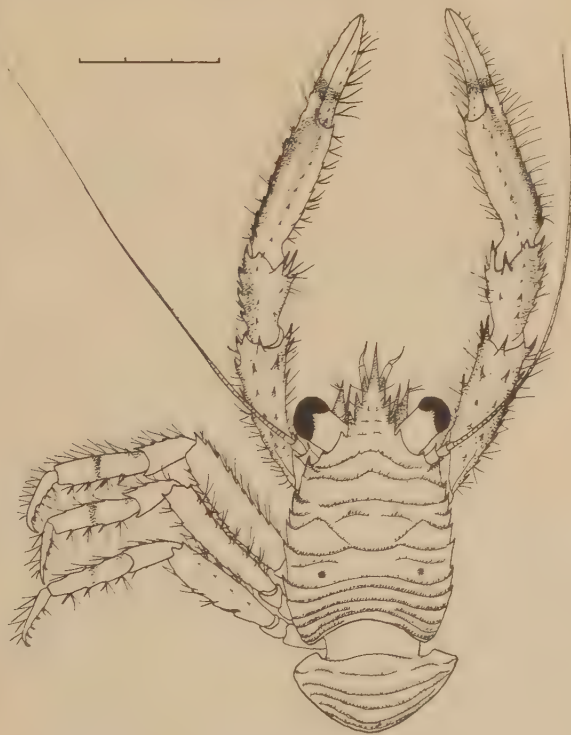


FIGURE 81.—*Galathea rostrata* Milne Edwards. Animal in dorsal view, walking legs of right side not shown, 3 mm. indicated.

squamiform, ciliated granules on surfaces; a few larger spines on carpus and distal end of merus; hand a little shorter than body; fingers gaping at base.

Abdomen with transverse striae like those on carapace but without spines.

Measurements.—Length of body: male, 18 mm.

Color.—Ground color off white, cream, and light yellow; mottled with orange and reddish orange especially on legs, less evident on body; spines red or tipped with red; a single small circular reddish spot in center of each branchial region; a white band on propodi of walking legs; distal half of fingers white (from specimen recently preserved in formalin).

Habitat.—Ten to 50 fathoms; (rarely to 1,178 fathoms south of Block Island, R.I.?).

Type locality.—Sixteen miles north of Jolbos Islands [Yucatan Peninsula] at 14 fathoms.

Known range.—Off Cape Hatteras, N.C., to off Mississippi River Delta, and Yucatan, Mexico; (Rhode Island?).

Remarks.—Reports of this species are rare in the literature and only a few specimens have been taken off Beaufort, N.C.

Ovigerous females have been reported off western Florida in March and April (Milne Edwards and Bouvier, 1897, and U.S. National Museum records).

Genus *Munida* Leach, 1820

Leach, 1820, p. 52.—Milne Edwards and Bouvier, 1897, p. 20 (rev.).

Munida irrasa Milne Edwards

Figure 82

Munida irrasa Milne Edwards, 1880, p. 49.—Hay and Shore, 1918, p. 402, pl. 28, fig. 8.—Chace, 1942, p. 46 (rev.).

Recognition characters.—Carapace narrowed anteriorly, adorned with iridescent pubescence, spiny. Rostral spine much longer than supraocular spines, latter not extending so far as cornea. A row of 10 spines across gastric region in addition to 1 or 2 on each hepatic region, 2 to 4 on each triangular area, and 1 to 4 on either side behind cervical groove on inner portion of each branchial region; anterolateral spine long, followed by 6 distinct lateral spines. Merus of third maxillipeds with three spines on lower margin.

Chelipeds three or four times as long as carapace, covered with squamiform, ciliated tubercles;



FIGURE 82.—*Munida irrasa* Milne Edwards. Animal in dorsal view (after Milne Edwards and Bouvier, 1897).

fingers agape at base; merus with rows of spines continued on carpus and hand. First pair of walking legs reaching proximal end of hand.

Abdomen without spines.

Measurements.—Length of carapace: males, 11 mm.; females, 14 mm.; smallest ovigerous female, 4 mm. (Chace, 1942).

Habitat.—Thirty to 260 fathoms.

Type locality.—Not designated with certainty.

Known range.—Off Cape Lookout, N.C.; Florida through West Indies to Grenada; Gulf of Mexico to Colombia and Venezuela; "600 mi. off St. Davids, Bermuda."

Remarks.—Ovigerous females have been taken off southeast Florida in July, and off North Carolina in September. The rhizocephalans *Cyphosacus chacei* and *Boschmaia munidicola* were reported from *M. irrasa* by Reinhard (1958).

Family Porcellanidae

General form crablike. Carapace well calcified, depressed, regions usually not well defined; front often prominent but never with rostrum greatly projecting beyond eyes. Antennae inserted external to eyes, with three movable articles and a flagellum. Basal articles of antennules broad. Outer maxillipeds too large to be contained in buccal cavity. Chelipeds moderately elongate, usually broad and depressed. First, second, and third walking legs well developed; last leg feeble, reduced in size, inflexed and resting on carapace. Abdomen broad, symmetrical, composed of seven segments, bent under and held closely against thorax; males with a pair of pleopods on segment two, sometimes rudimentary or absent, females with a pair of pleopods on segments three, four, and five, those on three sometimes reduced or absent. Telson composed of five or seven well-calcified pieces (Haig, 1960).

KEY TO GENERA AND SPECIES IN THE CAROLINA

(Modified after Chace, 1942)

- a. Form elongate, "hippalike"; telson much longer than broad.....*Eucramus praelongus* (p. 109).
- aa. Form less elongate; telson usually broader than long, never much longer than broad.
 - b. Lateral wall of carapace broken up into two or more pieces, separated by membranous interspaces; front triangular or transverse in dorsal view, never with projecting teeth; carapace subquadrate.
 - c. Carapace with numerous transverse tufts of setae; chelipeds and legs hairy
 - Pachycheles pilosus* (p. 108).
 - cc. Carapace relatively smooth, not hairy; chelipeds deeply ridged and eroded, not hairy
 - Pachycheles rugimanus* (p. 108).
 - bb. Lateral wall of carapace nearly always entire; if not, front distinctly tridentate in dorsal view; carapace not subquadrate.
 - c. Basal antennal article small, not joining margin of carapace, so that movable articles have free access to orbit.....*Petrolisthes galathinus* (p. 107).
 - cc. Basal antennal article strongly produced forward and broadly in contact with margin of carapace, movable portion far removed from orbit.
 - d. Dactyls of walking legs armed with from two to four strong, fixed spines; carapace distinctly broader than long----*Polyonyx gibbesi* (p. 113).

dd. Dactyls of walking legs ending in a simple spine usually with small, movable accessory spinules on lower margin; carapace longer than broad.

e. Front strongly tridentate in dorsal view; carapace slightly longer than broad; chelipeds not grossly sculptured.

f. Cervical groove terminating anterolaterally in shallow marginal indentation at edge of carapace.....*Porcellana sayana* (p. 110).

ff. Cervical groove terminating anterolaterally in a distinct longitudinal cleft at edge of carapace....*Porcellana sigsbeiana* (p. 111).

ee. Front strongly trilobate in frontal view; carapace usually broader than long; chelipeds thick and grossly sculptured

Megalobrachium soriatum (p. 112).

Genus *Petrolisthes* Stimpson, 1858

Stimpson, 1858, p. 240.—Haig, 1960, p. 21.

Petrolisthes galathinus (Bosc)

Figure 83

Porcellana galathina Bosc, 1801 (or 1802), p. 233, pl. 6, fig. 2.

Petrolisthes galathinus: Hay and Shore, 1918, p. 404, pl. 29, fig. 1.—Haig, 1956, p. 22 (rev.).—1960, p. 36.



FIGURE 83.—*Petrolisthes galathinus* (Bosc). Animal in dorsal view, fifth leg only of left side shown, 5 mm. indicated.

Recognition characters.—Carapace a little longer than wide, covered with strong, transverse, ciliated rugae, scarcely interrupted at grooves separating well-marked regions; frontal region granulate, metabranchial regions plicate. Front produced into a broad, triangular, sinuous-sided rostrum with a broad median groove usually covered with short pubescence. Supraorbital spine present, not distinct in large specimens; postorbital angle produced into a small spine-tipped tooth; epibranchial spine strong. Eyes well developed. Antenna with first movable article bearing an anteromedian, spine-tipped, lamellar lobe; second and third articles lightly rugose.

Chelipeds large, covered with strong, ciliated rugae continuing obliquely and almost unbroken across carpus and hand, broken into series of shorter rugae on fingers; merus with a strong rugose lobe at inner distal angle; carpus about twice as long as wide, anterior margin with four to six strong serrate spines, a row of spines on posterior margin; hand broad, flattened, rugae on outer margin spiniform in smaller specimens, outer margin often fringed with plumose hairs; dactyl sinuous, fingers closing closely, a thick tuft of pubescence below. Walking legs rugose; anterior margin of meri with fringe of plumose hairs; all articles covered with long, nonplumose setae; anterior margin of first and second legs with six to nine spines, third with five to seven; merus of first and second with a posterodistal spine.

Sternum, sternal plastron, abdomen, ventral surface of outer maxillipeds, chelipeds, and walking legs covered with strong striations.

Measurements.—Length of carapace: males, 7 to 17 mm.; non-ovigerous females, 6 to 11 (15?) mm.; ovigerous females, 7 to 14 mm. (Haig, 1960; Holthuis, 1959).

Color.—Grayish brown without markings in life; in alcohol, light brown with purple or dark-red lines and dots on rugae (Hay and Shore, 1918). Spaces between rugae yellow; lower surface, including abdomen, deep red (Faxon in Haig, 1960).

Habitat.—Under stones and associated with sponges, corals, and anemones in littoral; in somewhat deeper water, from sand and sand-shell bottom (Haig, 1960); low-water mark to 27 fathoms.

Type locality.—Unknown.

Known range.—Cape Hatteras, N.C., through Gulf of Mexico and Caribbean area to Rio de Janeiro, Brazil; Ilha Trinidad off Brazil; Pacific Ocean from region around Panama City; Isla San Lucas, Costa Rica; off La Libertad, Ecuador.

Remarks.—A full review of this species has been given by Haig (1956, 1960). Ovigerous females are known from the Caribbean area from January to May, and from North Carolina and the Gulf of Mexico from June to September (Haig, 1956, 1960; Holthuis, 1959, in part).

Rathbun (1926) described a fossil species, *P. avitus*, from the Pliocene of Central America which is similar to the recent *P. galathinus*.

Genus *Pachycheles* Stimpson, 1858

Stimpson, 1858, p. 228.—Haig, 1960, p. 131 (rev.).

Pachycheles pilosus (H. Milne Edwards)

Figure 84

Porcellana pilosa H. Milne Edwards, 1837, p. 255.

Pachycheles pilosus: Haig, 1956, p. 11 (rev.).

Recognition characters.—Carapace slightly broader than long, flattened but somewhat more convex from front to back than side to side, lightly rugose along sides, with numerous short, transverse tufts of setae except scattered setae on frontal region. Frontal margin sinuous, slightly produced in middle, with a submarginal row of stout setae. Anterolateral margins emarginate. Epimeral pieces of metabranchial regions separated by membranous interspaces, posterior por-

tion consisting of one or more pieces. Orbits deeply excavated, postorbital angle spiniform; eyes short, stout. Antenna with first movable article bearing a buttressed spine on anterior margin; second article with a spine near middle of anterior border; third article short, smooth.

Chelipeds unequal, stout, ornamented with numerous long, dark setae with shorter ones between; merus outlined dorsally with long setae, a stout spine and large white tubercle at inner distal angle; carpus with a number of prominent white tubercles on proximal portion, anterior border with about three spines; hand inflated, outer margin spined and tuberculate below and at base of immovable finger, fingers short, immovable finger with a single blunt tooth on cutting edge, inner edge of hand and dactyl with obsolescent spines. Walking legs with hairy covering similar to chelipeds, a few spines below on dactyls and propodi.

Telson of males and females with five elements.

Measurements.—Length of carapace: males, 7 mm.; ovigerous females, 5 to 7 mm. (Haig, 1956).

Habitat.—In corals; to 4 fathoms (Schmitt, 1935a).

Type locality.—Vicinity of Charleston, S.C.

Known range.—Charleston, S.C.; Key West to Sarasota Bay, Fla.; through West Indies to Tobago and Aruba.

Remarks.—Ovigerous females have been taken in the West Indies from February to May (Haig, 1956, in part). Rathbun (1926) reported a Pliocene species of *Pachycheles* from Central America.

Pachycheles rugimanus Milne Edwards

Figure 85

Pachycheles rugimanus Milne Edwards, 1880, p. 36.—Hay and Shore, 1918, p. 404, pl. 29, fig. 2.—Haig, 1956, p. 12 (rev.).

Recognition characters.—Carapace slightly longer than wide except in mature females, flat from side to side, convex from front to back, rugose along sides; anterolateral margins emarginate; epimeral pieces of metabranchial regions separated by membranous interspaces, posterior portion consisting of one or more pieces. Front broad, frontal margin projecting downward, slightly produced in middle, hardly visible from above. Orbits deeply excavated, margins slightly raised, postorbital angle spiniform; eyes short, stout, retractile. Antenna with first movable article bearing a serrate spine on anterior margin;

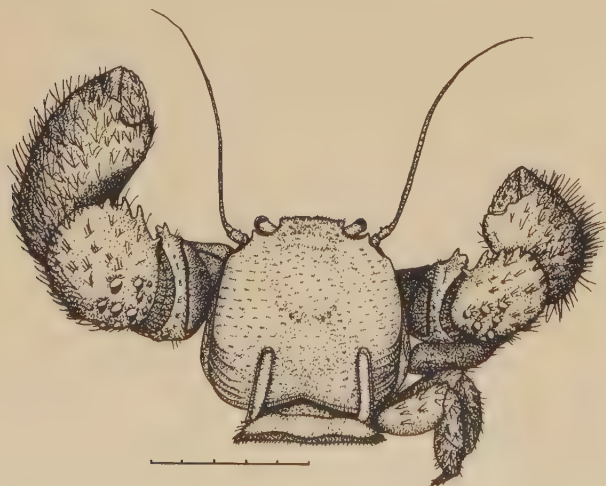


FIGURE 84.—*Pachycheles pilosus* (Milne Edwards). Animal in dorsal view, second, third, and fourth leg of left side not shown, 5 mm. indicated.



FIGURE 85.—*Pachycheles rugimanus* Milne Edwards. Animal in dorsal view, second, third, and fourth legs of left side not shown, 5 mm. indicated.

second article with a row of unequal spines on anterior border; third article short, smooth.

Chelipeds subequal, stout; merus crossed by a row rugae distally, a rugose and serrate spine at inner distal angle; carpus with four anterior spines, graded in size, proximal one largest, and upper surface with four prominent longitudinal, tuberculate ridges, with deep channels between, channels crossed by irregular septae forming rows of oblong pits between ridges; ridges and pitted channels continued on hand but with less regularity in arrangement; fingers tuberculate almost to tips. First three pairs of walking legs stout and with distal articles hairy; last legs weak and reflexed dorsally.

Telson of male and female with five elements; male pleopods present.

Measurements.—Carapace: male, length, 8 mm.; width, 7 mm.; ovigerous female, length, 8 mm., width, 9 mm.

Color.—Brownish red, fingers vermillion.

Habitat.—To depth of 79 fathoms (Schmitt, 1935a).

Type locality.—Contoy, and west of Florida.

Known range.—Off Cape Lookout, N.C., through Florida to St. Thomas, V.I., and Contoy Island, Mexico.

Remarks.—Only a few collections of this species have been recorded, from widely scattered localities. Ovigerous females have been taken in

February and March from the Carolinas and west Florida, and in September in North Carolina and east Florida.

Genus *Euceramus* Stimpson, 1860

Stimpson, 1860b, p. 445.—Halg, 1960b, p. 187.

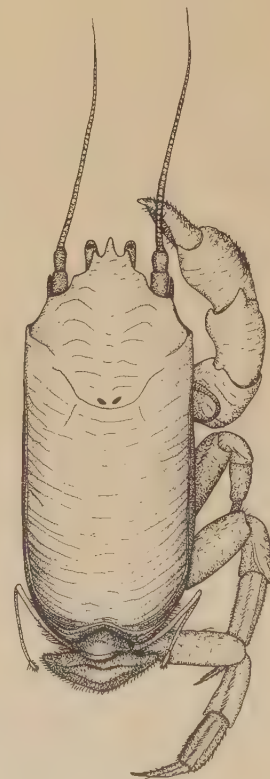
Euceramus praelongus Stimpson

Figure 86

Euceramus praelongus Stimpson, 1860b, p. 444.—Hay and Shore, 1918, p. 405, pl. 29, fig. 3.—Halg, 1956, p. 7 (rev.).

Recognition characters.—Carapace subcylindrical, elongate; sides slightly arcuate, with minute, irregular, transverse rugae; anterolateral margins with two more or less obtuse spines on each side behind antennae. Front tridentate, median spine about twice length of lateral spines, a broad V-shaped depression at rear edge of carapace. Eyes well developed. Antennule short. Antenna about three-fourths length of body, flagella sparsely covered with fine hairs; basal article short, not produced forward; movable articles not far removed from orbit. Third maxilliped large, forming subquadrate shield extending laterally almost to edge of carapace.

FIGURE 86.—*Euceramus praelongus* Stimpson. Animal in dorsal view, fifth leg only of left side shown, 5 mm. indicated.



Chelipeds stout, subequal; hand slightly roughened and hairy, somewhat stouter in males than in females; fingers about as long as palm, more gaping in males than in females. First pair of walking legs shorter than second and third pairs; last pair reduced and turned dorsally.

Abdomen small, distal segments narrow. Uropods reduced. Telson longer than broad, composed of seven elements.

Measurements.—Length of carapace from tip of rostrum to center of rear notch: males, 14 mm.; females, 14 mm.

Color.—Background of carapace greenish gray to greenish tan with lighter and darker lines of color delineating striae and marginal furrow; a light longitudinal stripe, broadest anteriorly, along middorsal line; purplish markings along lines separating major regions of carapace; legs mottled with greenish gray or tan as on carapace; a suggestion of iridescence on body and legs (from specimen collected by L. McCloskey, Morehead City Harbor, N.C., August 7, 1962).

Habitat.—Sandy beaches below waterline, and on broken-shell bottoms; low-water mark to 21 fathoms.

Type locality.—Beaufort, N.C.

Known range.—Chesapeake Bay, off South Marsh Island, to Aransas area of Texas coast.

Remarks.—Hay and Shore (1918) and Haig (1956) remarked that this is a rare species and it is true that it has seldom been collected, but the habits described by Pearse, Humm, and Wharton (1942) suggest that it is like a number of similar decapod crustaceans which are rare in collections chiefly because they live where they escape the attention of most collectors. Pearse, Humm, and Wharton described *E. praelongus* as a dweller of sandy beaches, similar in habit to *Emerita*, *Lepidopa*, and *Ogyrides*. It is also found on rubble-covered bottom. The animal is a highly adapted burrower which burrows backward. It scrapes food caught in the hairy antennae with setose mouth parts. Juvenile specimens are occasionally taken at night in plankton tows near inlets in North Carolina, and ovigerous females have been taken in May.

Haig (1960) placed *Euceramus* between the group of porcellanid "genera in which the basal antennal segment is short and not broadly in contact with the anterior margin of the carapace, and

the group of genera in which the basal segment is strongly produced forward so that the movable segments are far removed from the orbit."

Genus *Porcellana* Lamarck, 1801

Lamarck, 1801, p. 153.—Haig, 1960, p. 196 (rev.).

Porcellana sayana (Leach)

Figure 87

Pisidia sayana Leach, 1820, p. 54.

Porcellana sayana: Hay and Shore, 1918, p. 403, pl. 29, fig. 7.—Haig, 1956, p. 31 (rev.).

Recognition characters.—Carapace usually a little longer than wide, depressed; dorsal surface slightly convex, meeting lateral parts in a slight shoulder a little behind base of antenna; surface minutely granulate and with fine oblique dorsal plications along sides, especially on posterolateral portions; a few scattered small clumps of hairs. Rostrum triangular, concave above, tip abruptly decurved, margins spinulate or tuberculate. Orbit with a strong tooth near inner angle, separated from orbit by a wide and rather deep notch; outer angle produced into a broad, low tooth. Eyes well developed. Cervical groove lightly impressed. Antennae slender, smooth, longer than carapace; basal article strongly produced forward into a spinelike projection; movable articles far removed from orbit.



FIGURE 87.—*Porcellana sayana* (Leach). Animal in dorsal view, legs of left side not shown, 5 mm. indicated.

Chelipeds strong, heavy, finely plicate, nearly smooth in old individuals; hand as long as or longer than carapace, outer margin fringed with long hairs except in old individuals; fingers short, curved, and bent; proximal inner angle of carpus and distal inner angle of merus produced, forming lobes, both articles with scattered hairs near dorsolateral border, posterodistal angle of carpus ending in a spine. First three pairs of walking legs normal, with scattered hairs; last pair reduced and carried above others.

Telson composed of seven elements.

Measurements.—Carapace: males, length, 4 mm. (Wass, 1955), width, 12 mm.; nonovigerous females, length, 8 mm., width, 8 mm.; ovigerous females, length, 5 mm. (Haig, 1956) to 10 mm., width, 10 mm. Specimens with length and width equal are unusual.

Color.—Ground color reddish or rusty brown; covered on all dorsal surfaces and abdomen with complicated irregular pattern of yellowish white, yellow, and some bluish-white spots or longitudinal stripes; stripes more prominent on rear center part of carapace and on abdomen. Pattern quite variable in shape and shade, some specimens being predominantly light.

Habitat.—This species is often taken in the dredge in various parts of Beaufort Harbor, N.C., and along the neighboring coast. It has also been taken from among rocks of the jetties near Fort Macon. It is often found in crevices in clusters of oyster shells or as a commensal of the hermit crabs *Pagurus pollicaris* or *Petrochirus diogenes* in the shell of some gastropod. Hildebrand (1954) found specimens attached to the decorator crab, *Stenocionops furcata*. Shallow water to 48 fathoms; (390 fathoms(?), Schmitt, 1935a).

Type localities.—Coast of Georgia and Florida.

Known range.—Cape Hatteras, N.C., around Gulf of Mexico and Caribbean Sea to Bahia Caledonia, Panama; through West Indies to Venezuela and Surinam (Haig, 1956; Holthuis, 1959).

Remarks.—This species is rather abundant off the Carolinas and in the western Gulf of Mexico (Hildebrand, 1954, 1955). Ovigerous females are known to occur from January to November in various localities throughout the range. In North Carolina, they are known in January and from June to November. Brooks and Wilson (1883) described the first zoeal stage of *P. sayana*. A long

breeding season is indicated, as is true of a close relative in the Pacific, *Porcellana cancrisocialis*. Haig (1960) suggested that these forms may be conspecific.

Porcellana sigsbeiana Milne Edwards

Figure 88

Porcellana sigsbeiana Milne Edwards, 1880, p. 35.—Benedict, 1901, p. 137.—Milne Edwards and Bouvier, 1923, p. 292, pl. 1, fig. 6.—Haig, 1956, p. 33 (rev.).

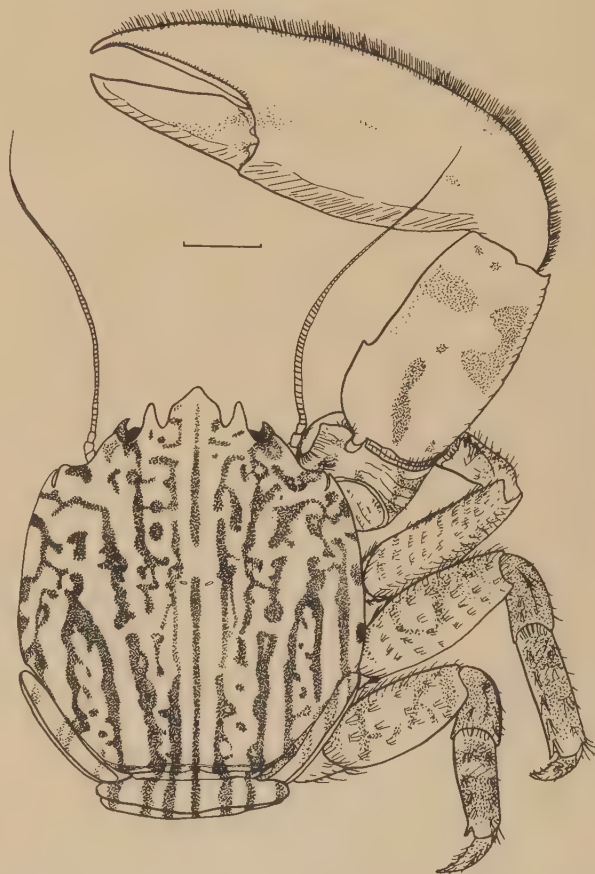


FIGURE 88.—*Porcellana sigsbeiana* Milne Edwards. Animal in dorsal view, fifth leg only of left side shown, 5 mm. indicated.

Recognition characters.—Carapace longer than wide, evenly convex in posterior half, broadly ridged in gastric region; lateral margins thin, produced, and slightly upturned; surface faintly rugose. Front strongly tridentate; rostrum exceeding narrower lateral teeth, irregularly pentagonal with sides adjacent to base subparallel. Orbit with outer angle produced into a broad, oblique tooth; eyes well developed. Anterolateral

borders concave, ending in a shoulder separated from acute marginal tooth by an elongate notch at terminus of cervical groove. Antennae slender, smooth, about as long as carapace; basal article strongly produced forward in a spinelike projection; movable articles far removed from orbit.

Chelipeds strong, heavy, smooth; hand longer than carapace, outer margin fringed with hairs; fingers less than half as long as palm, nearly straight, hooked at tips; length of carpus more than 1.5 times width, a single small spiniform tooth on anterior border; merus with a single broad tooth on lobe at internal angle. First three pairs of walking legs with scattered tufts of hairs; last pair reduced and carried above others.

Telson composed of seven elements.

Measurements.—Male carapace: length, 24 mm., width, 22 mm.

Color.—Colored with an irregular pattern of reddish longitudinal mottlings on a white background (specimens preserved in alcohol).

Habitat.—The species occurs near the edge of the Continental Shelf in North Carolina, and is usually found in deeper water than the related and similar species, *Porcellana sayana*; 27 to 215 fathoms.

Type localities.—Blake Stations: 49, off delta of Mississippi River, 118 fathoms; 36, north of Yucatan, 84 fathoms; 142, Flannegan Passage [V.I.], 27 fathoms.

Known range.—Off Marthas Vineyard, Mass., to northern Gulf of Mexico and southern Gulf of Mexico off Yucatan; West Indies to Virgin Islands.

Remarks.—Ovigerous females have been taken in April, May, June, and November off northwest Florida, Alabama, Mississippi, and Louisiana, and in midwinter off Yucatan. Benedict (1901) was correct in stating that this is the largest porcellanid species in the region.

Genus *Megalobrachium* Stimpson, 1858

Stimpson, 1858, p. 228.—Haig, 1960, p. 212.

Megalobrachium soriatum (Say)

Figure 89

Porcellana soriata Say, 1818, p. 456.—Hay and Shore, 1918, p. 404, pl. 29, fig. 6.

Porcellanopsis soriata: Haig, 1956, p. 35.

Megalobrachium soriatum: Haig, 1960, p. 227 (rev.).

Recognition characters.—Carapace somewhat hexagonal, slightly wider than long; margins

more or less hairy; areolations well marked, some tuberculate. Front rounded in dorsal view, trilobate in frontal view; rostrum little, if any, longer than lateral teeth. Orbits well defined; eyes well developed. Antennae about as long as carapace; basal article strongly produced forward and broadly in contact with margin of carapace; movable articles slender and removed from orbit.

Chelipeds long and heavy, roughly tuberculate; hand fringed with long hair along lower margin and with tubercles in rather well-defined rows; fingers with white, strongly hooked tips; carpus with one strong spine and some smaller spines on anterior border, dorsal aspect with tubercles irregularly arranged and appearing granulate under slight magnification; merus ornamented like carpus distally. First three walking legs stout, hairy, and with sharp, curved dactyls; last legs weak and placed above others.

Telson divided into five elements.

Measurements.—Carapace: length of male, 5 mm., width, 5.5 mm.; ovigerous females, length, 4 to 5 mm., width, 4 to 5.5 mm.

Color.—In life a dirty gray; in alcohol a rusty or grayish red.

Habitat.—Free living among corals, rocks, and sponges; in North Carolina found especially in canals of sponges taken from fishing banks offshore near Beaufort Inlet (Hay and Shore, 1918;



FIGURE 89.—*Megalobrachium soriatum* (Say). Animal in dorsal view, second, third, and fourth legs of left side not shown, 1 mm. indicated.

Pearse and Williams, 1951). Wass (1955) found the species in sponges of the genus *Ircinia* in Florida. Near low-water mark to 37 fathoms.

Type locality.—St. Catherines Island, Ga.

Known range.—Off Cape Hatteras, N.C., to Port Aransas, Tex.; West Indies to Barbados; Contoy, Mexico; Bahia Caledonia, Panama.

Remarks.—This small porcellanid crab has had a varied taxonomic history. First, Say's trivial name was misspelled by subsequent authors (*sociata* for *soriata*), as pointed out by Benedict (1901), and second, the generic designation has been changed four times as understanding of relationships has been variously interpreted. Chace (1942) shifted *soriata* from *Porcellana* to *Porcellanopsis*. The most recent reviser (Haig, 1960), after reviewing all species referred to *Megalobrachium* and *Porcellanopsis*, deemed it best to combine all forms in a single genus.

A close congener of the eastern Pacific is *M. tuberculipes* (Lockington), and Haig suggested that they may not be distinct.

Ovigerous females have been taken off the Carolinas in June, July, and August, and in July in Florida (Wass, 1955).

Genus *Polyonyx* Stimpson, 1858

Stimpson, 1858, p. 233.—Haig, 1960, p. 232.

Polyonyx gibbesi Haig

Figure 90

Porcellana macrocheles Gibbes, 1850, p. 191.

Polyonyx macrocheles: Hay and Shore, 1918, p. 405, pl. 29, fig. 8.

Polyonyx gibbesi: Haig, 1956, p. 28 (rev.).

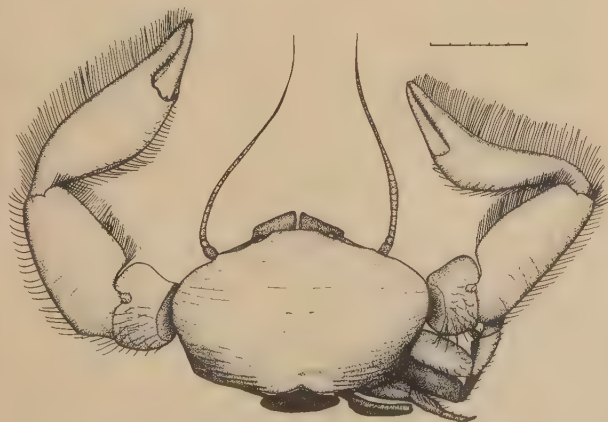


FIGURE 90.—*Polyonyx gibbesi* Haig. Female in dorsal view, second, third, fourth, and fifth legs of left side not shown, 5 mm. indicated.

Recognition characters.—Carapace smooth, finely plicate, transversely oval, about one-fourth to one-third wider than long; front hardly produced, margin slightly sinuous; posterolateral portions with scattered, feathered hairs; infolded lateral portions separated from rest of carapace by a deep fissure. Orbits small, eyes small, cornea reduced. Antenna slender, about 1.5 times as long as body; basal article strongly produced forward; movable articles far removed from orbit.

Chelipeds unequal, long and distorted; larger hand nearly twice as long as carapace; superior margin of hands convex, with thin fringe of plumose hairs, inferior margin nearly straight, with fringe of long plumose hairs; distal two-thirds of propodus with single row of fine, close-set, subtruncate teeth, larger and less closely set distally (row longer on small hand); fingers short, hooked at tip, toothed on cutting edges, dactyl falciform, sparsely hairy (straighter on small hand); carpus as long as palm, thick, anterior margin produced into a thin crest, proximal end markedly subrectangular, entire margin with fringe of fine plumose hairs, a thinner fringe of shorter hairs on outer margin; merus subcubical, finely rugose above, upper margin produced in front, plumose-hairy dorsolaterally. First three pairs of walking legs sparsely hairy, last pair with long tuft on chela and distal end of carpus; merus of second and third legs spinulose below, dactyls of first to third legs with four corneous spines on internal margin closing against weaker spines on distal portion of propodus.

Measurements.—Carapace: male, width, 11 mm.; nonovigerous female, length, 9 mm., width, 13 mm.; ovigerous female, width, 16 mm.

Color.—Grayish white, sometimes stained with brown.

Habitat.—A common commensal of the annelid *Chaetopterus variopedatus* [= *pergamentaceus*], seldom found outside tubes of this worm; intertidal to 8 fathoms.

Type locality.—Coast of South Carolina.

Known range.—Woods Hole, Mass.; Rhode Island; Beaufort, N.C., to Alligator Harbor, Fla.; Puerto Rico; Bahia Caledonia, Panama. Notes in Haig's (1956) account for *P. gibbesi* indicate that the species may range to Brazil.

Remarks.—It is unfortunate that this distinctive species, known so long under the name *Poly-*

onyx macrocheles (Gibbes), should have to undergo a name change, but Haig (1956) has shown that *Porcellana macrocheles* Gibbes, 1850, is a homonym of *Porcellana macrocheles* Poepig, 1836, hence unavailable. The substitute name is quite appropriate, however, for it not only honors the original describer but is applied to a species common in the area where he worked.

Unlike other porcellanids occurring in the Carolinas, *Polyonyx gibbesi* has been the subject of some ecological observations. Enders (1905), at Beaufort, N.C., and Pearse (1913), at Woods Hole, Mass., studied commensal inhabitants of the tubes of *Chaetopterus variopedatus*, finding *P. gibbesi* to be common commensals in both areas. Both authors found usually a male and a female crab in the same tube, but Enders found six isolated ovigerous females in the course of a summer. Pearse found the species to be strongly thigmotactic, and crabs, seemingly too large to enter *Chaetopterus* tubes, entered and left an artificial tube at will in the laboratory.

Individuals usually moved backward or sideways on open sand, using the chelipeds as an aid in walking, or at times swam clumsily upside down by flapping the abdomen. Individuals showed little ability to burrow. The respiratory mechanism seemed well adapted to life in confinement, for the respiratory currents were strong and capable of being directed, changing with the change in direction of waterflow in the worm tube. Crabs in an experimental tube tolerated considerable fouling of the water.

Pearse gave an excellent figure of the detailed structure of the chelate and tufted fourth walking legs which are used extensively in the meticulous preening characteristic of this species. The plumes of hairs on the appendages, especially those on the third maxillipeds, are used as nets for capturing food from water currents.

Gray (1961) reviewed the life history and ecology of the species. He found that the breeding season at Beaufort, N.C., extends at least from April to December, and ovigerous females are otherwise known in February and March from Florida. Usually when a pair of *P. gibbesi* is found in a tube, adult crabs of no other species are present at the same time. The smallest female with eggs was 8.4 mm. in width. Gray concluded

that the crabs enter worm tubes by chance, not in response to attractants.

In the years since Enders' and Pearse's studies, the proportion of *Pinnixa chaetoptera* to *Polyonyx gibbesi* at Woods Hole and Beaufort has changed. Woods Hole; *Polyonyx-Pinnixa*; 1913, 22:78; 1959, 66:34. Beaufort; 1905, 83:17; 1958-59, 39: 61. Gray (1961) postulated that the more southerly species, *P. gibbesi*, has increased in the Woods Hole area due to amelioration of climate. In the Beaufort area, decline may be due to recent hurricane damage which destroyed many *Chaetopterus* tubes. Gray also found that *P. gibbesi* prefers less muddy bottoms than *P. chaetoptera*. He considered *P. gibbesi* an obligate commensal of *Chaetopterus*.

Faxon (1879) discussed the last stage zoea of *P. gibbesi* and determined that it molts directly into the first crab stage with no intervening megalops as in brachyurans. Smith (1880b) reported swarms of zoeae of *P. gibbesi* at the edge of tidal currents near the mouth of Narragansett Bay in summer.

Superfamily Paguridea

Carapace elongate and subcylindrical, or broad and crablike; front not fused with epistome. Abdomen soft, asymmetrical, and spirally coiled, merely bent or flexed against thoracic sterna as in Brachyura, or rarely symmetrical, straight and well calcified dorsally. Tail fan usually present and asymmetrical, occasionally symmetrical. Eyes never in orbits. Antennal peduncle five jointed; second article almost always with a movable acicle. First pair of legs chelate and usually large; fifth pair always, and fourth pair commonly, much less developed than preceding pairs. Abdominal appendages usually unpaired on second to fourth, or second to fifth segments, and usually present only on left side (Alcock, 1905).

Family Paguridae. Hermit crabs

Carapace usually somewhat elongate and broadened posteriorly, sides membranous, and covered with a network of very thin lines ordinarily limited above by *linea anomurica*. Abdomen generally soft and spirally coiled in adaptation to gastropod shells (abdomen secondarily symmetrical in a few forms using other kinds of

housing). Eye scales triangular. Thoracic sternites, corresponding to third, fourth, and fifth legs, free and mobile. Legs four and five reduced and modified. Middle terga of abdomen separated more or less by membrane (adapted from Alcock, 1905; Bouvier, 1940).

Remarks.—A most useful bibliography of this group was published by Gordan (1956). The family Paguridae has a long fossil record in North America. Species of *Paguristes*, *Petrochirus*, and *Pagurus* are known from the Cretaceous, and *Dardanus* from the Eocene (Rathbun, 1935).

KEY TO SUBFAMILIES IN THE CAROLINAS

- a. Third maxillipeds approximated at base; chelipeds subequal, or left much larger than right, rarely with right slightly larger than left.....*Diogeninae* (p. 115).
- aa. Third maxillipeds widely separated at base by a sternum; right cheliped usually much larger than left, left never larger than right, occasionally subequal
Pagurinae (p. 125).

Subfamily Diogeninae

The chief distinguishing characters are given in the above key.

KEY TO GENERA AND SOME SPECIES OF DIOGENINAE IN THE CAROLINAS

- a. Paired appendages present on first two abdominal segments of male, and first abdominal segment of female; fingers of chelipeds opening and closing horizontally
Paguristes (p. 115).
- aa. No paired appendages on anterior abdominal segments in either sex.
 - b. Fingers of chelipeds opening and closing horizontally.....*Olibanarius vittatus* (p. 120).
 - bb. Fingers of chelipeds opening and closing obliquely or nearly vertically.
 - c. Chelipeds not markedly unequal, right usually slightly larger than left
Petrochirus diogenes (p. 122).
 - cc. Chelipeds markedly unequal, left much larger than right.....*Dardanus* (p. 123).

Genus *Paguristes* Dana, 1852

Provenzano, 1959, p. 381 (rev.).

KEY TO SPECIES IN THE CAROLINAS

- a. Rostrum broadly rounded, or pointed, but not advanced beyond level of lateral projections on front.
 - b. Anterolateral sides of anterior shield of carapace not spiny.....*moorei* (p. 115).
 - bb. Anterolateral sides of anterior shield of carapace definitely spiny.....*lymani* (p. 116).

- aa. Rostrum slender, and definitely advanced beyond level of lateral projections on front.
 - b. Anterior shield of carapace not noticeably longer than broad.
 - c. Frontal and lateral margins meeting at almost a right angle.....*sericeus* (p. 117).
 - cc. Frontal and lateral margins meeting at broadly obtuse or rounded angle.....*triangulatus* (p. 118).
 - bb. Anterior shield of carapace noticeably longer than broad.
 - c. Eye scales acuminate.....*spinipes* (p. 118).
 - cc. Eye scales with three or four (occasionally two) terminal spines.....*tortugae* (p. 119).

Paguristes moorei Benedict

Figure 91

Paguristes moorei Benedict, 1901, p. 144, pl. 4, fig. 3.—Hay and Shore, 1918, p. 409, pl. 30, fig. 3.

Recognition characters.—(Taken from holotypic female.) Anterior shield of carapace slightly longer than broad; upper surface of carapace with a few scattered hairs and irregular punctations, more or less iridescent. Rostrum short, obtusely pointed, slightly less advanced than more acute lateral projections. Eyestalks slender, slightly dilated distally, slightly longer



FIGURE 91.—*Paguristes moorei* Benedict. Type female, anterior part of body in dorsal view, approximately $\times 5$ (after Benedict, 1901).

than width of anterior shield (8.6 mm.); eye scales not adjacent, anterior process acute. Antennular peduncle slightly exceeding eyestalk when extended. Antennal peduncle extending slightly beyond middle of eyestalk; flagellum not exceeding tips of legs, with scattered setae; acicles bispinose at tip (right spine on right acicle broken), a row of four strong spines on proximal two-thirds of inner side (right acicle with a single external spine).

Chelipeds subequal but of similar form, medial margins nearly straight; hands short and thick, covered dorsally with many tubercles and hairs, but nearly smooth ventrally, a row of strong spines on upper medial border of palm, edges of fingers fitting closely; carpus similar to hands but with fewer tubercles in two rows, largest tubercles on medial upper border; merus prismatic with tubercles on angles. First pair of walking legs with a row of spines along upper margin of carpus and propodus.

Measurements.—Carapace (holotypic female): length in midline, 13.2 mm., width, 11.8 mm.; anterior shield, length, 8.5 mm., width, 8.3 mm.

Color.—Yellowish, eyestalks deep orange or crimson below, and white above (Hay and Shore, 1918).

Habitat.—From near edge of continental shelf in North Carolina.

Type locality.—Puerto Rico.

Known range.—Gulf Stream about 30 miles south of Cape Lookout, N.C.; Puerto Rico.

Remarks.—The species is known from only two specimens. The type only is extant.

Paguristes lymani Milne Edwards and Bouvier

Figure 92

Paguristes lymani Milne Edwards and Bouvier, 1893, p. 49, pl. 4, figs. 13–22.—Benedict, 1901, p. 145, pl. 4, fig. 8.—Alcock, 1905, p. 157.

Recognition characters.—Anterior shield of carapace slightly broader than long, sides a little hairy and roughened by spiny granules; postero-lateral corners notched. Rostrum often a rounded lobe falling far short of pointed lateral projections; front rounding gradually to lateral margins from lateral projections. Eyestalks somewhat dilated at base and longer than distance between apices of lateral projections of front; eye scales singly acuminate or with up to three unequal spines on anterior border, long hairs some-

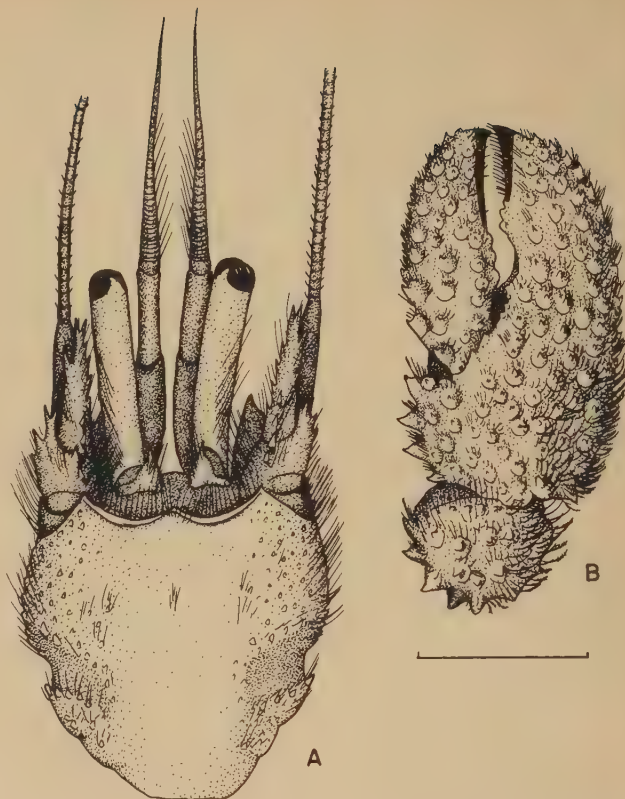


FIGURE 92.—*Paguristes lymani* Milne Edwards and Bouvier. A, anterior part of body in dorsal view; B, right chela, outer surface; 5 mm. indicated.

what obscuring tip. Antennular peduncles highly variable, exceeding eyestalks from less than half to entire length of terminal article. Tips of antennal peduncles extending to base of cornea, or slightly beyond eyes; acicles extending to three-fourths length of eyestalks, terminated by a spiny fork and often with three to five spinules on internal or external borders, external spine at base of acicle also spinulose on outer margin.

Chelipeds small, subequal, and similar; hands about twice as long as broad, upper surface covered with rather large tubercular granules, many with corneous tips, and four spines on internal margin of palm; lower margin of palm concave at base of immovable finger; fingers slightly agape, terminated by corneous tips preceded by finely denticulate cutting edges, dactyl with four or five small teeth behind corneous portion; carpus with three rows of spines on upper surface, four or five large ones on inner margin, about six on outer margin (with distalmost largest), and

about six more on upper surface near inner margin; superior border of merus armed with more or less pointed projections, feebly rugose externally; spines of palm, carpus, and merus obscured by feathered hairs. Walking legs with long hairs, particularly on upper and lower borders of dactyls; spines on crest of carpus, propodus, and base of dactyl, and somewhat reduced ones on inner and outer sides of propodus and carpus where rows appear mixed with hairs; dactyls arched, somewhat shorter than combined length of two preceding articles, and terminated by a conical claw.

Measurements.—Length of carapace: males, 13 mm.; ovigerous females, 11 mm.

Variations.—The spination of the chelipeds may vary in strength and density. The length of the antennular peduncles, in relation to the eyestalks, is highly variable. The eye scales become more dentate with age [implied]. The rostrum may reach the level of the lateral projections of the front, and small individuals tend to be hairier than large ones (Milne Edwards and Bouvier, 1893).

Habitat.—Literature and museum records show that this species has been found housed in small to medium-sized shells belonging to the families Cassididae, Dentaliidae, Nassariidae, Ovulidae, Muricidae, Trochidae, Turridae, and Volutidae; 15 to 878 fathoms.

Type locality.—Sand-Key, [Fla.], 15 fathoms.

Known range.—Southeast of Cape Lookout, N.C. (82–100 fathoms); Florida Keys to Swan Island off Honduras; through West Indies to British Guiana.

Remarks.—Ovigerous females have been taken in February from North Carolina and Florida, in May and June from Florida, and in November from British Guiana.

Paguristes sericeus Milne Edwards

Figure 93

Paguristes sericeus Milne Edwards, 1880, p. 44.—Milne Edwards and Bouvier, 1893, p. 46, pl. 3, figs. 14–22.—Provenzano, 1961, p. 155.

Paguristes rectifrons Benedict, 1901, p. 145, pl. 4, fig. 7.

Recognition characters.—Anterior shield of carapace nearly as broad as long, flattened, with several spines on each side; frontal margin as long as ocular peduncles, making nearly a right angle with lateral margins; lateral projections

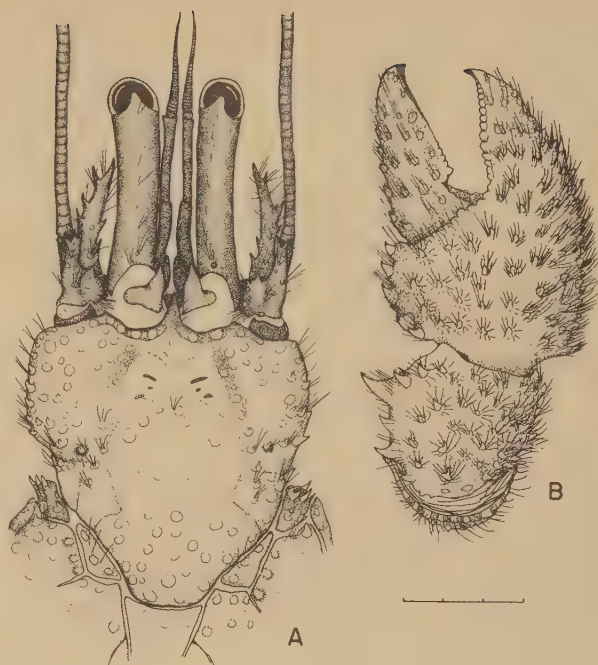


FIGURE 93.—*Paguristes sericeus* Milne Edwards. A, anterior part of body in dorsal view; B, right chela, outer surface; 3 mm. indicated.

low but terminating in a small spine. Rostrum with acute tip reaching along approximately half length of eye scales. Ocular peduncles slightly narrowed in middle; eye scales small, acuminate at tip. Antennular peduncles extending almost to tips of eyestalks. Antennal peduncles slightly exceeding acicles, terminal article armed with two spines; acicles straight, terminated by a spiny fork and with two or three spines on internal and external borders.

Chelipeds subequal, and rather short and broad; upper surface of hands and carpi with soft, silky, yellow hairs nearly obscuring surface, many strong granulations becoming corneous at tips scattered over upper surface. Walking legs not reaching much beyond extended chelipeds; dactyls regularly curved, dactyl of first walking leg 1.5 times length of propodus, of second as long as propodus and carpus combined.

Measurements.—Length of carapace: approximately 20 mm. (Milne Edwards and Bouvier, 1893).

Variations.—There is apparently some variation in straightness of the front and length of the eyestalks, as judged by the accounts of Milne

Edwards and Bouvier (1893) and Benedict (1901).

Color.—Body reddish with white spotting; eyestalks not spotted but solid orange red (from recently preserved specimen and from Provenzano, 1959, 1961).

Habitat.—Coral rubble and sand; found in *Strombus*, *Murex*, and *Oliva* (Provenzano, 1961, and various authors); 5 to 36 fathoms.

Type locality.—Lat. 24°34' N. long. 83°16' W. [near Dry Tortugas, Fla.], 36 fathoms.

Known range.—Off Cape Lookout, N.C.; Florida Keys to Virgin Islands.

Remarks.—Ovigerous females are known from the Virgin Islands in April (Provenzano, 1961).

Paguristes triangulatus Milne Edwards and Bouvier

Figure 94

Paguristes triangulatus Milne Edwards and Bouvier, 1893, p. 40, pl. 4, figs. 6–12.—Benedict, 1901, p. 146, pl. 4, fig. 9.—Alcock 1905, p. 157.

Recognition characters.—Carapace somewhat hairy toward sides, and with scattered hairs on anterior shield; shield a little longer than broad; front with a thickened margin and a pointed rostrum reaching well beyond broadly angular lateral projections. Eyestalks long, slightly dilated, but obliquely compressed at tips, a line of hairs along dorsal side; eye scales acuminate, a little rugose on internal border. Antennular peduncles with about half of terminal article extending beyond eyestalks. Anternal peduncles extending to base of cornea or as little as three-fourths length of eyestalks; acicles reaching about to middle of eyestalks, spinose on internal and external borders, tip often bifurcate.

Chelipeds subequal, similar, upper surfaces tuberculate and hairy; inner margin of hands, carpi, and bases of dactyls with strong spines corneous at tips; upper surfaces of carpi and meri with a few spines and spiniform tubercles corneous at tips. First walking legs with spiny crest on carpi, propodi, and base of dactyls, crest obsolescent on second pair, both pairs hairy dorsally; dactyls curved, about as long as two preceding articles together; dactyls of right side a little weaker than left and laterally compressed; proximal end of first left dactyl with cross section in form of curvilinear triangle, broadly rounded internal face serving as base and obtusely pointed

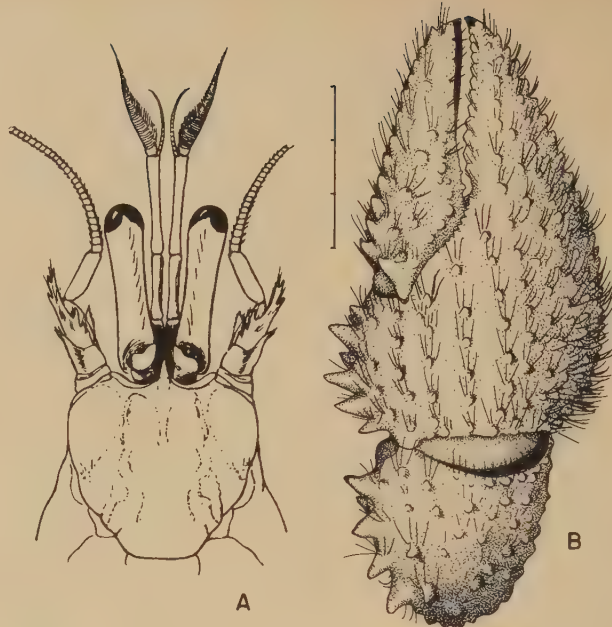


FIGURE 94.—*Paguristes triangulatus* Milne Edwards and Bouvier. A, anterior part of body in dorsal view, approximately $\times 3$ (after Benedict, 1901); B, right chela, outer surface, 3 mm. indicated.

external face serving as apex; second left dactyl a little stronger.

Measurements.—Length of carapace: male, 11 mm.; ovigerous female, 12 mm.

Color.—Legs and anterior part of cephalothorax tinted pink (Milne Edwards and Bouvier, 1893); eyestalks pink (Benedict, 1901).

Habitat.—One specimen has been reported from a shell of *Murex* (Milne Edwards and Bouvier, 1893); 6.5 to 82 fathoms.

Type locality.—Barbados, 73 fathoms.

Known range.—Off Oregon Inlet, N.C. (6.5 fathoms); Tortugas, Fla.; Barbados; Trinidad.

Remarks.—Ovigerous females have been taken from Florida in August and October.

Paguristes spinipes Milne Edwards

Figure 95

Paguristes spinipes Milne Edwards, 1880, p. 44.—Milne Edwards and Bouvier, 1893, p. 33, pl. 3, figs. 1–13.—Benedict, 1901, p. 145, pl. 4, fig. 6.—Alcock, 1905, p. 157.—Boone, 1927, p. 76. *Paguristes visor* Henderson, 1888, p. 78, pl. 8, fig. 3. *Paguristes armatus* Hay, 1917, p. 73.—Hay and Shore, 1918, p. 409, pl. 30, fig. 7.

Recognition characters.—Anterior shield of carapace convex, considerably longer than broad; frontal margin thickened and drawn out into an almost straight-sided, acute rostrum, with tip con-

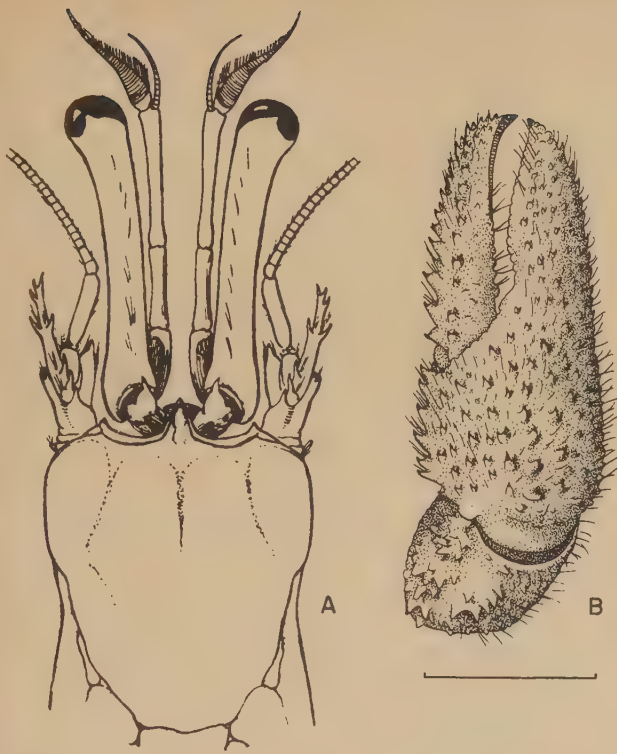


FIGURE 95.—*Paguristes spinipes* Milne Edwards. A, anterior part of body in dorsal view, approximately $\times 4$ (after Benedict, 1901); B, right chela, outer surface, 5 mm. indicated.

siderably exceeding rather obtuse lateral projections. Eyestalks considerably longer than greatest width of front but not quite so long as length of anterior shield, somewhat contracted in middle and slightly bent laterally, not much dilated distally; eye scales acuminate. Antennular peduncles extending to tips of, or a little beyond, eyestalks. Antennal peduncles extending about two-thirds length of eyestalks; acicles straight, terminated by a spiny fork, and with two or three spines on internal and external borders.

Chelipeds subequal and similar in form, narrow but massive; hands less than half as broad as long; upper surface of hands and carpi covered with conical spines, many with corneous tips, strongest on superointernal border; fingers more than half as long as whole of propodus and terminating in corneous tips, opposed edges with numerous teeth. Walking legs extending a little beyond chelipeds, ornamented with tufts of hair most numerous and rigid on dactyls; dactyls regularly curved and half again as long as pro-

podus; crest of spines on carpus and propodus extending along a portion of dactyl of first walking legs, but reduced, and present on carpus only of second walking legs.

Measurements.—Length of carapace: adults, 17 mm.; immatures, approximately 5 mm. (Milne Edwards and Bouvier, 1893, in part).

Variations.—The eyestalks are somewhat shorter than the front in young individuals but much longer in adults; they are frequently unequal in length. The cardiac region is calcified but the areas lateral to it are variably calcified (Milne Edwards and Bouvier, 1893).

Color.—A spot of orange red on external and internal faces of first walking legs, less definite on two following pairs; occasionally, traces of red coloration on anterior part of cephalothorax (Milne Edwards and Bouvier, 1893). In alcohol, nearly white, each cheliped with a conspicuous orange-yellow band across merus and a faint trace of a similar band on each walking leg (Hay and Shore, 1918).

Habitat.—This essentially deep-water hermit has been taken from shells of *Cassis* and *Xenophora*; 73 to 350 fathoms.

Type locality.—Grenada, 92 fathoms.

Known range.—Gulf Stream south of Cape Lookout, N.C., off Cape Canaveral and Sarasota, Fla.; Barbados to Pernambuco, Brazil.

Remarks.—This species has rarely been collected north of Barbados.

Paguristes tortugae Schmitt

Figure 96

Paguristes tortugae Schmitt, 1933, p. 7, fig. 4.—Provenzano, 1959, p. 388, fig. 11 (rev.).

Recognition characters.—Anterior shield of carapace longer than broad; rostrum triangular, in advance of lateral projections of front. Eyestalks slender, straight, as long as greatest width of anterior shield; eye scales separated by rostrum, anterior process armed with three or four spines (occasionally two) decreasing in size from median spine outward. Antennular peduncles reaching to base of cornea or slightly beyond. Antennal peduncles reaching to three-fourths length of eyestalks; flagella not reaching to tips of chelipeds, sparsely setose; acicles obscured by hairs, armed with two spines on inner edge and at least three on outer edge.



FIGURE 96.—*Paguristes tortugae* Schmitt.
Anterior part of body in dorsal view,
× 10 (after Holthuis, 1959).

Chelipeds equal, thickly covered with hairs, medial margins of chelae and carpi straight, fitting closely together when retracted; hands with forwardly directed, hooked spines on median upper surface, inner margin, outer half, and outer margin of immovable finger, hairs arising along anterior part of base of tubercles giving a squamose appearance; dactyl with seven more or less distinct, transverse rows of small, horny-tipped tubercles, largest on upper margin; fingers with tips corneous, more or less spooned; lower surface of chela smooth except for some tufts of hairs. First and second walking legs with heavy fringes of hairs along upper and lower margins and some tufts on lateral surfaces, outer surface smooth;

dactyls somewhat longer than propodi, tips dark, corneous, a row of similar colored spinules on ventral border; inner surface of dactyls and propodi with squamiform tubercles near upper and lower margins, more pronounced where bases of hairs coincide with squamous tubercles. First walking legs with upper surface of propodus serrate, and a few denticles at base of dactyl. Second legs with two rows of spines on carpus, one on upper margin and one on upper portion of inner surface, a shallow groove on upper part of inner surface extending distad from carpus. Third legs with a single row of spines on carpus; merus of second and third legs with an anteroventral spine.

Measurements.—Length of carapace: male, 10 mm.; ovigerous female, 7 mm. (Provenzano, 1959).

Variations.—Holthuis (1959) described a somewhat longer rostrum, a longer antennular peduncle, a somewhat spinier acicle, and a less spiny merus on the cheliped for Surinam specimens.

Color.—Whitish, with large spines on inner margin of hand and carpus red; occasionally, hard parts lightly tinted with green or purple; eyestalks with a single band of black on white, and antennules with similar rings on ends of articles (Provenzano, 1959). In preserved material, these dark bands appear red (Holthuis, 1959).

Habitat.—Usually taken on hard or shelly bottom; shallow water to 20 fathoms.

Type locality.—Off Fort Jefferson Dock, Garden Key, Dry Tortugas, Fla.

Known range.—Reefs off Beaufort, N.C., to southern Florida; through West Indies to Surinam.

Remarks.—Ovigerous females have been reported from February to October in Florida (Provenzano, 1959, in part), in June in North Carolina, August in South Carolina, October in Puerto Rico, and in May from Surinam (Holthuis, 1959).

Genus *Clibanarius* Dana, 1852

Dana, 1852, p. 6.

Clibanarius vittatus (Bosc). Striped hermit crab

Figure 97

Pagurus vittatus Bosc, [1801 or 1802], p. 78, pl. 12, fig. 1.
Clibanarius vittatus: Hay and Shore, 1918, p. 410, pl. 30, fig. 9.—Provenzano, 1959, p. 371, fig. 5 D.

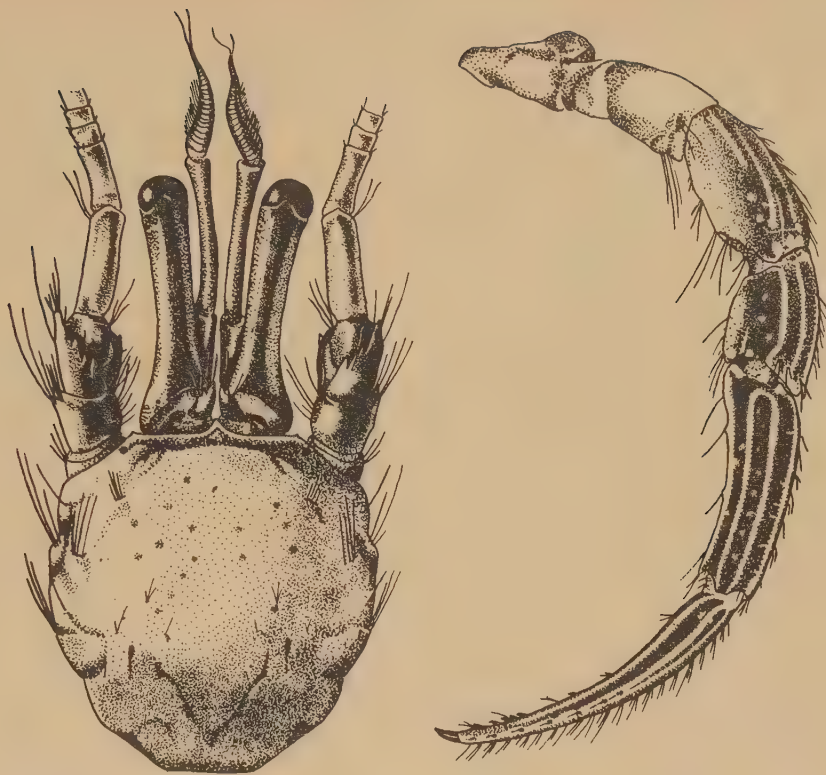


FIGURE 97.—*Clibanarius vittatus* (Bosc). A, anterior part of body in dorsal view, $\times 1.6$; B, third leg, $\times 3.2$ (after Holthuis, 1959).

Recognition characters.—Anterior shield of carapace subquadrate, a few fine hairs along lateral margin. Front with rostrum acute, triangular, slightly more prominent than lateral projections. Eyestalks almost as long as width of anterior shield, nearly cylindrical, cornea not dilated, right eyestalk occasionally slightly shorter than left; eye scales narrow, approximated at tips, but well separated at bases, margin with one to four spines, terminal largest. Antennular peduncles as long as eyestalks. Antennal peduncles reaching to at least three-fourths length of eyestalks; acicles acute, with three to five terminal spines, flagella reaching tips of walking legs.

Chelipeds equal, sparsely hairy; hands thick, inflated, twice as long as broad, covered thickly above, sparingly below, with somewhat blunted spines darker than color of hands and with bundles of stiff hairs springing from bases; fingers opening horizontally, heavy, toothed and somewhat gaping at base, cutting edges corneous, extending along upper side; carpus as long as

palm. First and second walking legs exceeding chelipeds by over half length of dactyls, tips corneous; two distal articles with numerous bundles of hairs. Third and fourth walking legs reduced; third subchelate; fourth very small, chelate, and turned on back.

Measurements.—Length of carapace: male, 32 mm.; female, 29 mm.

Color.—Greenish to dark brown with longitudinal stripes of gray to white; antennular peduncles light above, dark laterally, with orange flagella; propodus of walking legs with four pairs of light, longitudinal stripes continuous with similar stripes on dactyl and carpus, one of ventral stripes usually somewhat diffuse (Provenzano, 1959).

Habitat.—Common on harbor beaches, especially on borders of mud flats (Pearse, Humm, and Wharton, 1942); often on rock jetties or high on bay shores (Whitten, Rosene, and Hedgpeth, 1950); waterline to a few feet.

Type locality.—Coasts of Carolina.

Known range.—Potomac River, Gunston, Va., to Rio de Janeiro, Brazil.

Remarks.—This large species is one of the commonest conspicuous hermit crabs of the shore region of the Carolina bays. It has a broad range along the western Atlantic, and Holthuis (1959) has given new distribution records, as well as a history of its early recognition in this hemisphere.

Ovigerous females have been reported from Surinam in July and August (Holthuis, 1959) and from Florida in October (Provenzano, 1959).

Genus *Petrochirus* Stimpson, 1858

Stimpson, 1858, p. 233 (71).

Petrochirus diogenes (Linnaeus)

Figure 98

Cancer Diogenes Linnaeus, 1758, p. 631.

Petrochirus bahamensis: Hay and Shore, 1918, p. 410, pl. 30, fig. 6.—Schmitt, 1935a, p. 206, fig. 66.—Provenzano, 1959, p. 378, fig. 8.—1961, p. 153 (rev.).

Petrochirus diogenes: Holthuis, 1959, p. 151 (rev.).

Recognition characters.—Anterior shield of carapace flattened, as broad as long, rough, uneven, and with scattered tufts of hairs; front trilobate, rostrum about as long as lateral projections. Eyestalks straight, dilated distally, with a tuft of hair above corneal surfaces and scanty tufts near base; eye scales broad basally, acute anteriorly with indistinct serrations. Antennular peduncles reaching or exceeding eyestalks. Antennal peduncles shorter than eyestalks; acicles slender, hairy, and minutely spined.

Chelipeds massive, subequal, right slightly larger; hands and carpi coarsely roughened with grouped tubercles separated by appressed setae on upper and, to some extent, lower surfaces, becoming spinose along inner margin; fingers opening obliquely, major chela with fingers tuberculate on crushing edges, minor chela with fingers somewhat spooned, cutting edges sharp, tips corneous. First two pairs of walking legs with carpus ornamented above like chelae; propodi similar with clusters of hairs beneath; dactyls with slightly twisted rows of spines and dense setae; propodi and carpi, especially of first walking legs, with dorsal row of dark-tipped spines. Third legs subchelate; last legs chelate and turned up against side.

Measurements.—Length of carapace: male, 75 mm.; female, 44 mm.



FIGURE 98.—*Petrochirus diogenes* (Linnaeus). Female in dorsal view showing well-developed triramous pleopods, $\times 0.35$ (after Provenzano, 1959).

Color.—Generally reddish; chelipeds reddish except between fingers, and white spots on carpal articles; antennal and antennular peduncles longitudinally striped with red and white, antennal flagella transversely banded with red and white (Provenzano, 1959).

Habitat.—Mud, mud and shell, and sand bottoms. Common on shrimping grounds near Tortugas, Fla. (Provenzano, 1959), in the western Gulf of Mexico (Hildebrand, 1954, 1955), and on fishing grounds southeast of Cape Lookout, N.C., in about 18 fathoms; to 50 fathoms (Provenzano, 1959; Holthuis, 1959).

Type locality.—Near shores of Bahama Islands (Catesby, in Holthuis, 1959).

Known range.—Off Cape Lookout, N.C., to Brazil; West Indies.

Remarks.—The genus *Petrochirus* has a fossil record extending from the Cretaceous to the pres-

ent in North America (Rathbun, 1935). Toulou (1911) considered the Miocene form from Panama to be conspecific with the living species in the West Indies region, but Rathbun (1918a) considered this form as distinct (*P. bouvieri*) and possibly ancestral to the modern species.

Petrochirus diogenes is the largest hermit crab in the Carolinian fauna and this feature, plus its coarsely tuberculate, ruddy appendages, makes it conspicuous. A common commensal is the porcelainid crab, *Porcellana sayana*, and other commensals on the shells carried by the crab, such as *Crepidula plana* (Say), bryozoans (*Scrupocellaria* sp.), tubicolous worms (*Hydroides* sp. and *Spirorbis* sp.) and other species, are mentioned by Pearse (1932b). Ovigerous females have been reported in March from the Virgin Islands (Provenzano, 1961).

Pearse (1932a) determined the freezing point of *P. diogenes* blood (range -1.90° to -2.32° C.).

Holthuis (1959) reviewed the complex nomenclatural history of the species, designated the type, restricted the type locality, and delimited the geographic range.

Genus *Dardanus* Paulson, 1875

Paulson, 1875, p. 96 (translation).—Hemming, 1958b, p. 163.—Provenzano, 1959, p. 372.

KEY TO SPECIES IN THE CAROLINAS

- a. Propodus of second left walking leg conspicuously hairy, with a lateral longitudinal ridge paralleled by a groove, ridge crossed by rugae.....*venosus* (p. 123).
- aa. Propodus of second left walking leg not hairy, without a lateral longitudinal ridge or groove, rugae arranged in herringbone pattern.....*insignis* (p. 124).

Dardanus venosus (H. Milne Edwards)

Figure 99

Pagurus venosus H. Milne Edwards, 1848, p. 61.

Dardanus venosus: Verrill, 1908, p. 441, text-figs. 58-59; pl. 26, figs. 4a, 5a.—Provenzano, 1959, p. 374, fig. 6 (rev.).

Recognition characters.—Anterior shield of carapace slightly longer than width of front, smooth, with few hairs and some deep lines near sides; anterior margin with rostrum wanting, lateral projections between bases of eyestalks and antennae prominent. Eyestalks stout, slightly constricted in middle, extending to tips of antennal peduncles or slightly beyond, a tuft of setae just behind cornea; eye scales widely separated, inner margins straight, blunt tips bearing

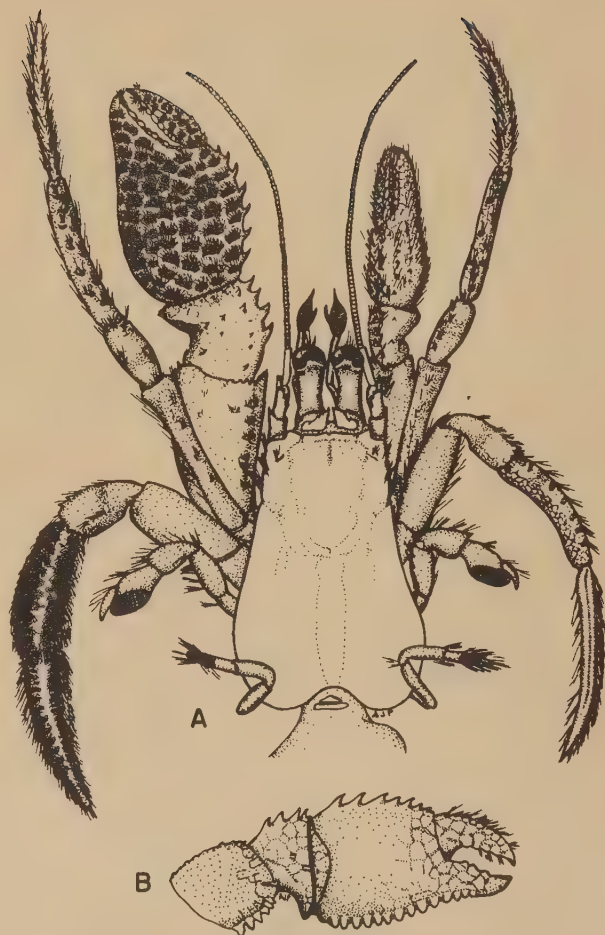


FIGURE 99.—*Dardanus venosus* (H. Milne Edwards). A, anterior part of body in dorsal view showing ridge on second left walking leg; B, inner surface of major chela showing "veins" which specific name describes; A-B approximately $\times 1.5$ (after Provenzano, 1959).

several spines. Antennular peduncles exceeding cornea by one-third of terminal peduncular article. Acicles short, reaching midlength of eyestalks, armed with small, sharp spines.

Chelipeds unequal, left much larger than right; fingertips black, corneous, spooned. Major chela with outer surface covered by scalelike tubercles separated by fan-shaped fringes of appressed hairs, inner surface smooth, medial margin bearing row of seven sharp, horny-tipped spines continued as row of smaller spines on dactyl and as well-developed spines on carpus; carpus with smaller sharp spines scattered over surface. Minor chela narrower, lacking scalelike tubercles on outer surface, and with long setae rather than appressed bristles. Walking legs with dactyls

longer than propodi, longest in first pair; second left leg markedly different from others, with dactyl and propodus broadened, fringed with hairs, and with a lateral longitudinal ridge paralleled by a groove, ridge crossed with numerous rugae.

Measurements.—Length of carapace (medium sized individual): 31 mm. (Verrill, 1908).

Color.—Walking legs with broad, transverse bands of red; legs, fingers of hands, and inside surfaces of chelipeds reticulated with fine red lines (hence, descriptive specific name); scalelike tubercles of hand and rugae of second left leg blue to purple; eye scales sometimes white (Provenzano, 1959).

Habitat.—Often found on sand and grass flats, on mud bottom, and in baited traps (various authors). Shells inhabited sometimes bear sponges or coelenterates (Holthuis, 1959). Shallow water near shore to 50 fathoms; rarely to 200 fathoms.

Type locality.—Guadeloupe.

Known range.—Off Beaufort Inlet, N.C. (Cerame-Vivas, Williams, and Gray, 1963); through West Indies to northeastern Brazil; Bermuda.

Remarks.—Ovigerous females have been reported from northeastern Florida in June, from the Virgin Islands in March and May (Provenzano, 1961), and from northeastern South America in April, May, July, and September.

Dardanus insignis (Saussure)

Figure 100

Pagurus insignis Saussure, 1858, p. 453, pl. 3, figs. 20, 20a.
Dardanus insignis: Verrill, 1908, p. 446, text-fig. 60; pl. 26, figs. 4 b, c, 5b.

Recognition characters.—Anterior shield of carapace longer than width of front, with scattered clumps of setae, and roughened slightly near anterior and anterolateral margins. Anterior margin with rostrum wanting; lateral projections on front triangular, thickened, prominent, and hairy on frontal edge. Eyestalks stout, slightly constricted in middle, extending almost to tips of antennal peduncles, a pencil of hairs at base of dilated cornea; eye scales prominent, well separated, serrated distally with a strong medial pair of spines separated from a smaller more lateral series of four spines by a notch obscured by a pencil of setae. Antennular peduncles with base of terminal article exceeded by eyestalks. Acicles

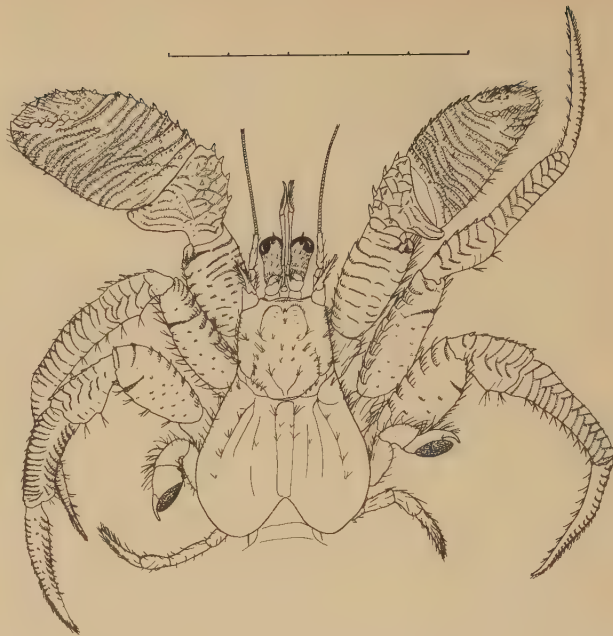


FIGURE 100.—*Dardanus insignis* (Saussure). Anterior part of male in dorsal view; 50 mm. indicated.

long, reaching to base of cornea, with a few spines and hairs arranged in a spiral line originating on inner surface at base and curving across dorsal surface to termination on lateral surface near tip.

Chelipeds heavy, left larger than right, covered with ciliated, tuberculate rugosities becoming bolder and more diagonal distally on hands and immovable fingers; movable finger of major chela with ciliated rugosities somewhat diagonal, those on minor dactyl irregularly arranged; opposed edges of fingers with heavy white teeth, tips black; spine on crest of meri, outer surface of carpi, and hands, largest spines on upper medial border; a row of spines on lower medial border of merus and ischium. First two pairs of walking legs strong, with rugose pattern similar to chelipeds and forming herringbone pattern on outer surface of propodus of large second left walking leg; dactyls of these walking legs with crest of spines dorsally, that of second left leg with crest of spines dorsally and ventrally, and continued below on propodus. Third and fourth walking legs reduced and specialized.

Measurements.—Male: length of carapace, 38 mm.; anterior shield, length, 17.5 mm., width, 15.5 mm.

Color.—Ground color yellowish; rugosities tan near body, becoming maroon on chelipeds and

first two pairs of walking legs distally, proximal rugae on hands with reticulate maroon pattern on yellowish background; anterior shield mottled tan; eyestalks banded alternately with maroon, yellow, and tan.

Habitat.—Fifteen to 124 fathoms.

Type locality.—Guadeloupe.

Known range.—Off Oregon Inlet, N.C., 17 fathoms (Cerame-Vivas, Williams, and Gray, 1963), to Port Aransas, Tex.; through West Indies to Guadeloupe.

Remarks.—Until recently this species was known only from beyond the 100-fathom curve in the Carolinas, but it has been collected in shallow water north of Cape Hatteras (Cerame-Vivas, Williams, and Gray, 1963).

Subfamily Pagurinae

The chief distinguishing characters for this group are given in the Key to Subfamilies of Hermit Crabs.

KEY TO GENERA OF PAGURINAE IN THE CAROLINAS

- a. Fingers opening and closing horizontally; no paired appendages on abdomen of either sex.
 - b. Vas deferens of male not protruding in form of a tube.....*Pagurus* (p. 125).
 - bb. Vas deferens of left side protruding, and coiled in a spiral.....*Spiropagurus dispar* (p. 133).
- aa. Fingers opening and closing obliquely; vas deferens of male not protruding; a pair of appendages on first abdominal segment of female only
 - Pylopagurus* (p. 133).

Genus *Pagurus* Fabricius, 1775

Provenzano, 1959, p. 393.—Hemming, 1958b, p. 163.

KEY TO SPECIES IN THE CAROLINAS

- a. Eye scales unarmed or with single subterminal spine.
 - b. Length of eyestalk not more than 3.5 times its greatest width.
 - c. Width of major chela less than one-half length.
 - d. Chelipeds subcylindrical, relatively smooth on outer surface; eye scales somewhat rounded distally, dorsal surface shallowly excavated.....*longicarpus* (p. 125).
 - dd. Chelipeds not subcylindrical, relatively spiny on outer surface; eye scales rounded distally but not excavated on dorsal surface.....*defensus* (p. 127).
 - cc. Width of major chela more than one-half length, one or both chelae broad and flattened.
 - d. Dactyl of major chela with sharply produced angle on medial margin; no depressed spot at base of immovable finger of either chela.....*pollicaris* (p. 128).

dd. Dactyl of major chela without sharply produced angle on medial margin; a depressed spot (or spots) at base of immovable fingers of chelae.....*impressus* (p. 129).

bb. Length of eyestalk at least 4 times its greatest width.....*annulipes* (p. 130).

aa. Eye scales armed with two or more spines.

b. Rostrum acute.....*pygmaeus* (p. 131).

bb. Rostrum obsolete.....*brevidactylus* (p. 132).

Pagurus longicarpus Say

Figure 101

Pagurus longicarpus Say, 1817, p. 163.—Hay and Shore, 1918, p. 411, pl. 29, fig. 3.—Provenzano, 1959, p. 394, fig. 13 (rev.).

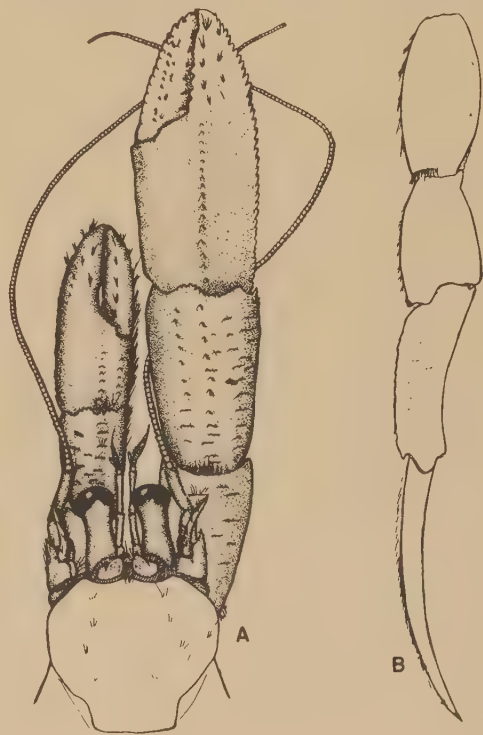


FIGURE 101.—*Pagurus longicarpus* Say. A, anterior part of body and chelipeds in dorsal view; B, second left walking leg in lateral view; A-B $\times 4$ (after Provenzano, 1959).

Recognition characters.—Anterior shield of carapace subcordate, truncate posteriorly, about as broad as long. Rostrum obsolete, hardly as advanced as lateral projections of front. Eyestalks stout, 2–3 times longer than broad, much shorter than width of anterior shield, cornea dilated; eye scales with concave, oval anterior lobe armed with a subterminal spine. Antennular peduncles exceeding eyes by about half length of terminal article. Antennal peduncles exceeding eyes by

about one-third length of last article; acicles slender, curved sinuously outward, reaching to tip of cornea; flagella exceeding tip of major cheliped.

Right cheliped much larger and longer than left, subcylindrical, devoid of hairs except for a few short setae along inner edges of fingers; width of hand less than one-half total length, palm lightly crested and minutely dentate along outer margin, upper surface minutely granulate and with two incomplete rows of larger granules near proximal end; fingers short, hooked at tips; carpus as long as propodus to middle of finger, with two rows of subspinous tubercles and scattered smaller ones. Left cheliped smaller, hairier, similarly formed but relatively broader; fingers with cutting edges distally, gaping at base. First and second walking legs with dactyls longer than propodi, extending about as far as chelipeds. Third and fourth pairs of legs reduced in size, fourth turned upward on back.

Measurements.—Length of carapace: male, 10 mm.; ovigerous female, 11 mm.

Color.—Color varies with locality; specimens of west Florida are lighter than those of east coast; upper surface of chelipeds and all walking legs iridescent; posterior carapace light green; hand white with median diffused pigment stripe, carpus with dorsal stripe and one on each side; walking legs with dactyl unstriped, propodus with lateral stripe, merus with single lateral muddy brown stripe and transverse stripe from lower anterior margin to broad pigmented area on upper surface; antennae with dark bands alternating with shorter white bands. Young may have transverse band on each article of walking legs rather than stripe; lateral stripes of major cheliped with V-shaped appearance in dorsal view (Provenzano, 1959, from west Florida specimen).

Habitat.—Common on harbor beaches, in harbor channels, and in shallow littoral on a variety of bottoms; to 27.5 fathoms (possibly beyond).

Type locality.—"Inhabits Bay Shores" [east coast of United States].

Known range.—Minas Basin, Nova Scotia (Rathbun, 1929) to northern Florida; Sanibel Island, Fla., to coast of Texas (Provenzano, 1959; Whitten, Rosene, and Hedgpeth, 1950).

Remarks.—*Pagurus longicarpus* is one of the commonest decapod crustaceans in shallow water

along the coast of the Eastern United States. Like other similarly available crustaceans, it has been the subject of a number of ecological and physiological studies, and these have been accomplished mostly around Woods Hole, Mass. Provenzano (1959) suggested that the Atlantic coast and Gulf of Mexico forms, with a hiatus between their ranges, may be subspecifically distinct.

The general habitat of *P. longicarpus*, summarized above, has been commented upon by other authors (Pearse, Humm, and Wharton, 1942; Allee, 1923). Allee concluded that the ubiquity of this hermit crab prevents it from being of aid in distinguishing shallow-water communities. Diatoms, detritus, and algae make up the food of this species (Sanders, Goudsmit, Mills, and Hampson, 1962).

The breeding season of this common form extends from early May to mid-September (Bumpus in Sumner, Osburn, and Cole, 1913b) in Massachusetts, and ovigerous females have been taken in January, March, and September in Florida (Wass, 1955, in part). Thompson (1901, 1903) described four zoeae, a glaucothoe, and a first postlarval stage, as well as various adolescent stages. He compared larval development of *P. longicarpus* with that of *P. annulipes* and gave remarks on the derivation and geological age of pagurids.

Autotomy and regeneration in this species received attention from Morgan (1900, 1901) and Haseman (1907), though investigations on this subject with other species now supersede the early studies. The first three pairs of legs have a fracture joint near their bases; hence, can be autotomized, but the last two pairs lack these and cannot be autotomized. Injuries distal to the fracture plane result in autotomy and regeneration; those proximal to the plane do not result in autotomy. Injured abdominal appendages are readily regenerated. Haseman carried this work farther, showing that when the chelipeds were removed at their breaking joints they differentiated from the tip proximally, but the first two pairs of clawed (walking?) legs differentiated from the base toward the tip. Direction of differentiation in the cheliped can be reversed by injuring the developing bud.

In another vein, conditioned and natural behavior of *P. longicarpus* has been the subject of a few

studies. Spaulding (1904) found the crab able to profit by experience in vision and taste experiments, and able to learn faster than *P. pollicaris*. Fink (1941) was able to demonstrate deconditioning of fear-reflex activity over a period of 18 days, the older crabs responding more slowly than young ones. Allee and Douglass (1945) found that a shell-less *P. longicarpus* would not feed, but if it were given a shell to occupy it would feed normally. Crabs in shells fight for food, the larger often fending smaller ones from a food supply. Movement from small to larger shells is accomplished only after several trials and thorough investigations of new shells, but shell-less crabs will accept almost any shape of shell in any condition. Shell-less crabs placed in a finger bowl tend to fight continuously until one or both are dead, usually within 24 hours. If an empty shell is dropped into a container with two shell-less crabs, one will immediately enter the shell. If the larger individual does not enter first, it will extract the smaller forcibly and enter in its place. Shell-less crabs will attack housed individuals regardless of size, but attackers were never seen to be successful when the two combatants were of equal size or when the housed individual was the larger.

Kropp and Perkins (1933) showed that in *P. longicarpus* and other remotely related decapods the chromatophore activity substance in the eyestalk will induce contraction of chromatophores in other species, and postulated that the substance is genetically similar throughout the group.

Finally, Reinhard (1944, 1945) and Reinhard and Buckeridge (1950) discussed parasitism in *P. longicarpus*. An examination of 8,000 crabs showed a 1-percent infestation with a larval acanthocephalid belonging to the genus *Polymorphus*. The worm was found in the abdominal cavity(?) usually attached to the hind gut or sometimes among tubules of the hepato-pancreas. The usual number of cysts per host was one, though as many as three occurred. Reinhard also described an entoniscid isopod, *Paguritherium alatum*, from this species. Entering the crab's body through the dorsal side of the eyestalk, and remaining in contact with this point of entry, the parasite elongates with but little damage to thoracic organs, but becomes greatly distended in the abdominal region. There it restricts the hepato-pancreas and nearly obliterates the gonads as it

grows. Infestation does not externally modify the male host. In females, the parasite reduces size of the first three pleopods, especially length of the endopod, and causes partial or complete loss of ovigerous hairs on the external surface of the endopod and protopod. Thus, secondary sexual characters of the female crab are altered. One percent of the crabs investigated were infested with this parasite.

Pagurus defensus (Benedict)

Figure 102

Eupagurus defensus Benedict, 1892, p. 7.

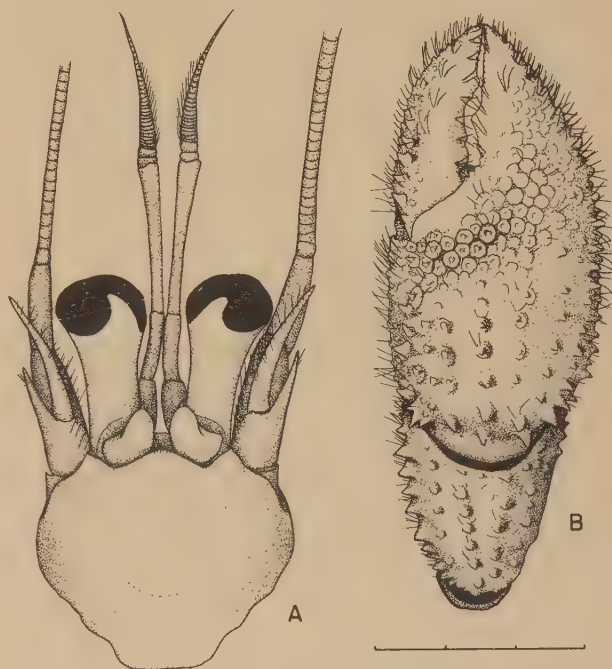


FIGURE 102.—*Pagurus defensus* (Benedict). A, anterior part of female in dorsal view; B, right chela, outer surface; 3 mm. indicated.

Recognition characters.—Anterior portion of carapace broader than long, subcordate. Rostral projection broadly rounded, lateral processes triangular, armed at apex with a short spine. Eyestalks stout, much dilated and flattened distally; eye scales broad, rounded, anterior margin forming a semicircle, armed with a subterminal spine. Antennular peduncles extending beyond eyestalks by two-thirds or more length of terminal article. Antennal peduncle extending beyond eyestalks by one-half length of terminal article; acicle curving outward and extending somewhat beyond eyestalk.

Chelipeds unequal, right larger than left. Major chela a little wider than carpus, fingers agape, margins set with comb of long, slender spines; upper surface with more or less diagonal rows of spines on palm and spines irregularly but closely set near base of dactyl and on immovable finger; dactyl with several rows of irregularly placed plates, and a small spine arising from center of each; carpus with three rows of sharp spines, one on outer margin, one on upper surface, and one on inner surface. Minor chela extending to base of major dactyl; hand armed with spines as in opposite member but hairier, and no spine-bearing plates on dactyl; fingers agape; carpus with a double crest of spines, outer margin convex, inner margin straight and flat; merus compressed. Walking legs long and slender, dactyls lightly setose, longer than preceding two articles together; propodus and carpus with a crest of spines.

Measurements.—Length of carapace: female, 7 mm.

Variations.—Fingers of the chelae do not gape in small individuals.

Habitat.—Sixteen to 49 fathoms.

Type locality.—Gulf of Mexico between Delta of Mississippi River and Cedar Keys, Fla., 30 fathoms.

Known range.—Cape Hatteras to Cape Lookout, N.C.; Tortugas, Fla., to Alabama.

Pagurus pollicaris Say

Figure 103

Pagurus pollicaris Say, 1817, p. 162.—Hay and Shore, 1918, p. 411, pl. 30, fig. 1.—Provenzano, 1959, p. 401, fig. 16 (rev.).

Recognition characters.—Anterior shield of carapace subcordate, nearly as long as broad, truncate posteriorly. Rostrum slightly less advanced than lateral projections of front. Eye-stalks moderately stout, not so long as width of anterior carapace, nearly straight, cornea dilated; eye scales with round-tipped, slightly concave anterior lobe armed with inferior subterminal spine. Antennular peduncles exceeding eyestalks by approximately half length of last article. Antennal peduncles exceeding eyestalks; acicles slender, curved outward, reaching to or beyond base of cornea, hairy medially.

Chelipeds unequal, right much larger than left, both covered with small, closely spaced granules, outer margins with enlarged granules or small

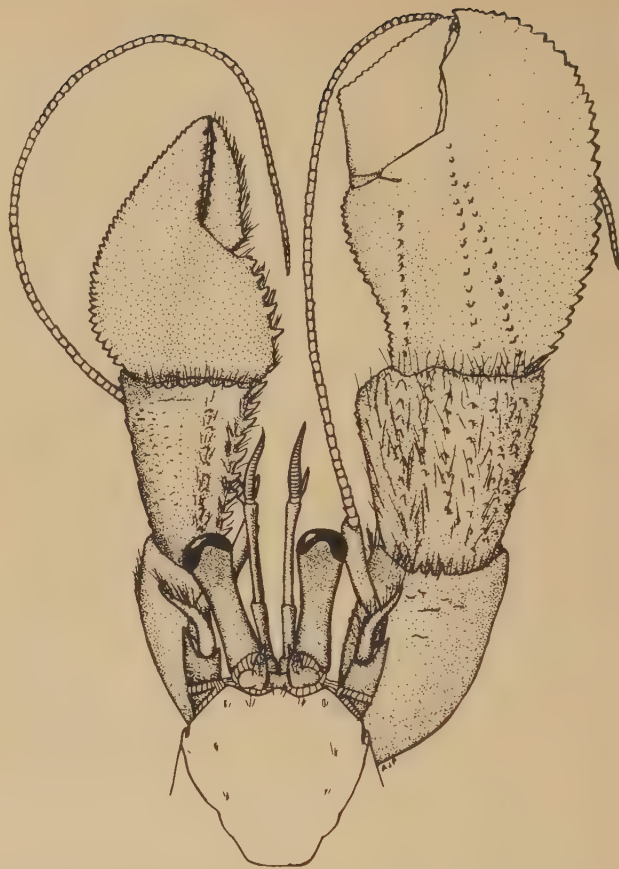


FIGURE 103.—*Pagurus pollicaris* Say. Anterior part of animal and chelipeds in dorsal view, approximately $\times 3$ (after Provenzano, 1959).

spines. Major chela stout, hand flattened; movable finger with prominent, projecting angle on medial border; tips of fingers acuminate; carpus with numerous tubercles, larger than on hand, subspinose and ciliated on upper surface; merus with a few squamiform tubercles. Minor chela with inner border dentate, movable finger not produced, dentation of inner border continued on inner dorsal border of carpus. First and second walking legs with dactyls much longer than propodi; first pair with small, well-defined spines along upper margin of propodus and carpus; second pair with spines reduced. Third legs reduced, fourth pair reduced and carried on back.

Measurements.—Length of carapace: male, 31 mm.; female, 27 mm.

Color.—Color varies with locality, those of west Florida being lighter than those of Northeastern States. Chelipeds basically white with gray margins on insides, tips of dactyls and dark area in

center of upper surface of each cheliped; remainder of body light gray-tan; eyestalks brown below cornea; hairs on antennules rusty brown (Provenzano, 1959, for west Florida form).

Habitat.—Deep channels of harbors and littoral waters; also found in shallow estuaries near ocean; near low-tide mark to 25 fathoms.

Type locality.—[East] coast of United States.

Known range.—Vineyard Sound, Mass., to northeastern Florida; Key West, Fla., to Texas (Provenzano, 1959).

Remarks.—Blake (1953) reported *P. pollicaris* from the Pleistocene of Maryland.

Ovigerous females have been reported in March from Florida (Provenzano, 1959). They have been found in January and November in North Carolina, and in April in Chesapeake Bay.

***Pagurus impressus* (Benedict)**

Figure 104

Eupagurus impressus Benedict, 1892, p. 5.

Pagurus impressus: Provenzano, 1959, p. 399, fig. 15 (rev.).

Recognition characters.—Anterior shield of carapace about as broad as long, flattened. Rostrum much rounded, in line with somewhat more angular lateral projections of front. Eyestalks slender, about three times longer than greatest width, cornea dilated and flattened; eye scales with moderately slender, acuminate, slightly excavated anterior lobe, subterminal spine large. Antennular peduncles exceeding eyestalks by at least half of last article. Antennal peduncles slightly exceeding cornea; acicles curving outward, reaching to base of cornea, hairy on medial edge.

Chelipeds unequal, right much larger than left, upper surfaces dented, both covered with small, closely crowded granules, outer margins bearing enlarged granules or small spines. Dactyl of major cheliped with a rounded angle on medial border near tip followed by marginal spines or granules, tips of fingers acuminate; carpus with five longitudinal rows of small spines often obscured by irregularly arranged additional spines, a row of well-developed spines along inner edge. Minor cheliped reaching to angle of major dactyl; a row of spines along inner margin of hand and carpus; fingers somewhat spooned at tips, cutting edges well defined, tips corneous, dactyl with medial border tuberculate; carpus with several rows of small spines. First and second walking legs with

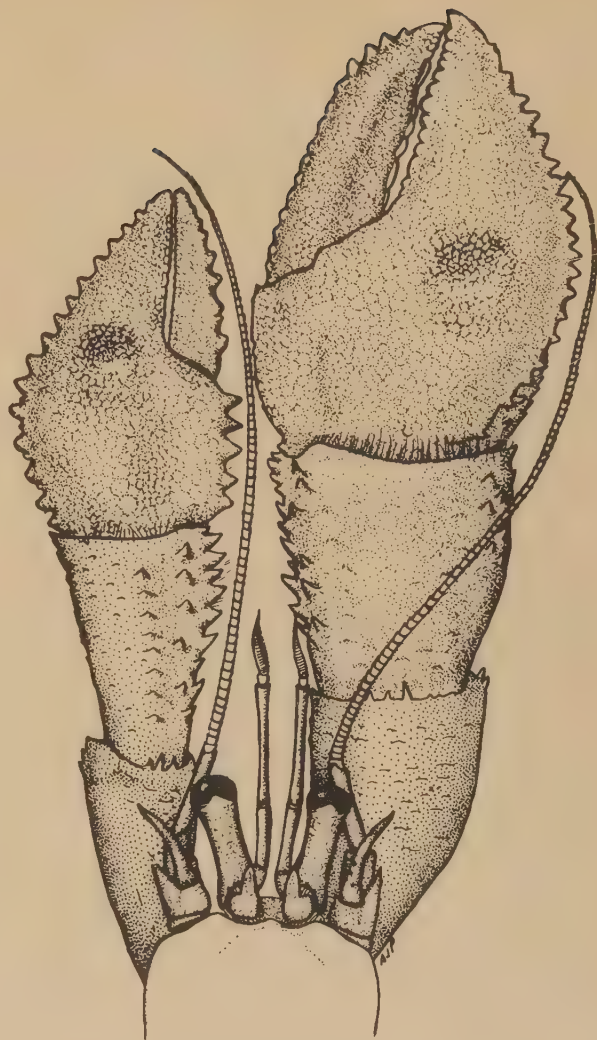


FIGURE 104.—*Pagurus impressus* (Benedict). Anterior part of body in dorsal view, approximately $\times 2.5$ (after Provenzano, 1959).

dactyls much longer than propodi; first pair with row of small, well-defined spines along upper margin of propodus and carpus; second pair with spines reduced. Third legs reduced, fourth reduced and turned on back.

Measurements.—Length of carapace: male, 25 mm.; female, 16 mm. (Provenzano, 1959).

Color.—Hands solid rust to chocolate brown, other appendages brownish with alternating thin bands of light color; antennae, antennules, and peduncles yellow; eyestalks brown above, bright blue below with bright scarlet at base of eyestalks (Provenzano, 1959).

Habitat.—On sandy bottom, grassy flats, or pilings; occasionally found in sponges (Wass, 1955); 6 to 18 fathoms.

Type locality.—Florida.

Known range.—Off Diamond Shoals, N.C., to east coast of Florida; western Florida from Sanibel Island north to vicinity of Alligator Harbor; Port Aransas, Tex.

Remarks.—Ovigerous females have been taken in January and February in the Carolinas.

Pagurus annulipes (Stimpson)

Figure 105

Eupagurus annulipes Stimpson, 1860a, p. 243.

Pagurus annulipes: Hay and Shore, 1918, p. 412, pl. 29, fig. 12 (rev.).—Provenzano, 1959, p. 407, fig. 18 (rev.).

Recognition characters.—Anterior shield of carapace subcordate, scarcely longer than wide, truncate posteriorly. Rostrum obsolete, about as long as rounded lateral projections of front. Eyestalks nearly straight, shorter than front, slightly constricted in middle, cornea not dilated; eye scales flat, broad, and rounded but with one or two spines on anterior border. Antennular peduncles exceeding eyestalks by about one-third of last article. Antennal peduncles reaching about to, or beyond, tip of eyestalks; acicles slender, curving outward, reaching about middle of last article of antennal peduncle; flagella exceeding major cheliped.

Chelipeds unequal, right much larger than left. Major cheliped long, subcylindrical, moderately and evenly granulate and ciliate above, except subspinose in large individuals; tips of fingers hooked, dactyl less than one-half length of hand; carpus nearly twice as long as broad, spinulose along inner margin. Minor cheliped much shorter, compressed, thickly ciliate and spinulose above; hand slightly shorter than carpus; fingers shorter than palm, with cutting edges distally, gaping at base. First and second walking legs with dactyls longer than propodi, legs slender, compressed; carpus with a distal spine on upper border. Third legs much reduced; fourth pair smaller, turned on back.

Measurements.—Length of carapace: male, 5 mm.; female, 4 mm. (Provenzano, 1959); Wass (1955) found a specimen with a carapace length of 7 mm.

Variations.—This is a small species. Males tend to attain larger sizes than females, and this is

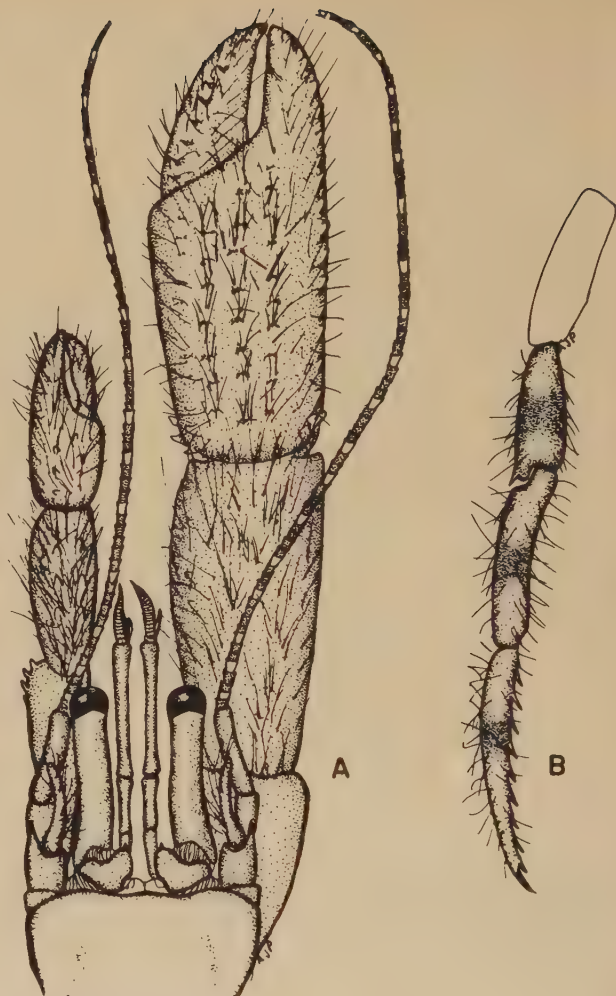


FIGURE 105.—*Pagurus annulipes* (Stimpson). A, anterior part of body and chelipeds in dorsal view; B, second left walking leg showing characteristic color bands in lateral view; A-B approximately $\times 7$ (after Provenzano, 1959).

accompanied by a proportionately larger cheliped (Provenzano, 1959).

Color.—White to gray with brown pigment band around each article of walking legs; antennae with broad purple bands alternating with narrower white bands, occasionally with poorly defined longitudinal stripes on legs (Provenzano, 1959).

Habitat.—Fairly common on a variety of bottom types in Massachusetts, but not so common in the Beaufort Harbor area of North Carolina; abundant in *Thalassia* beds in southern Florida, seemingly preferring soft, sandy bottom to other

types; tolerates somewhat lowered salinities of estuaries; near low-tide mark to 23 fathoms (Schmitt, 1935a).

Type locality.—Beaufort Harbor, N.C.

Known range.—Vineyard Sound, Mass., around Florida peninsula to Alligator Harbor; Cuba; Puerto Rico.

Remarks.—Ovigerous females have been reported in September from Massachusetts (Thompson, 1903), and from February to April, and August to September in Florida (Provenzano, 1959). Thompson described four zoeal, a glaucothoe, a postlarval, and a number of adolescent stages at Woods Hole. The only difference he found between *P. annulipes* and *P. longicarpus* in larval development was the slightly smaller size of the former.

Pagurus annulipes may occur a few miles offshore, for it has been found in the stomachs of flounders (*Paralichthys dentatus*) taken 15 miles east-southeast of Oregon Inlet, N.C., in 20-fathom water along with numerous juvenile *Cancer irroratus*.

***Pagurus pygmaeus* (Bouvier)**

Figure 106

Eupagurus pygmaeus Bouvier, 1918, p. 11, fig. 4.

Pagurus pygmaeus: Provenzano, 1959, p. 410, fig. 19.

Recognition characters.—Anterior shield of carapace longer than wide. Rostrum acute, slightly in advance of lateral projections, each bearing a terminal spine. Eyestalks shorter than width of anterior carapace, wide at base, tapering toward cornea; eye scales armed along medial margin with four or five spines. Antennular and antennal peduncles extending slightly beyond cornea; unarmed acicle reaching base of cornea.

Chelipeds unequal, right much larger than left, both with long but very fine hairs and forward-projecting spines. Major chela suboval, margin armed with strong spines, upper surface covered with smaller, nearly blunt spines; carpus with six very sharp spines on upper anteromedial surface, two additional spines more laterally placed, and a short row of spines along lateral margin. Minor chela much reduced, twice longer than broad, upper surface with many blunt spines, some forming two central rows; tips of fingers corneous, spooned; carpus with double row of large spines on upper surface. Walking legs with

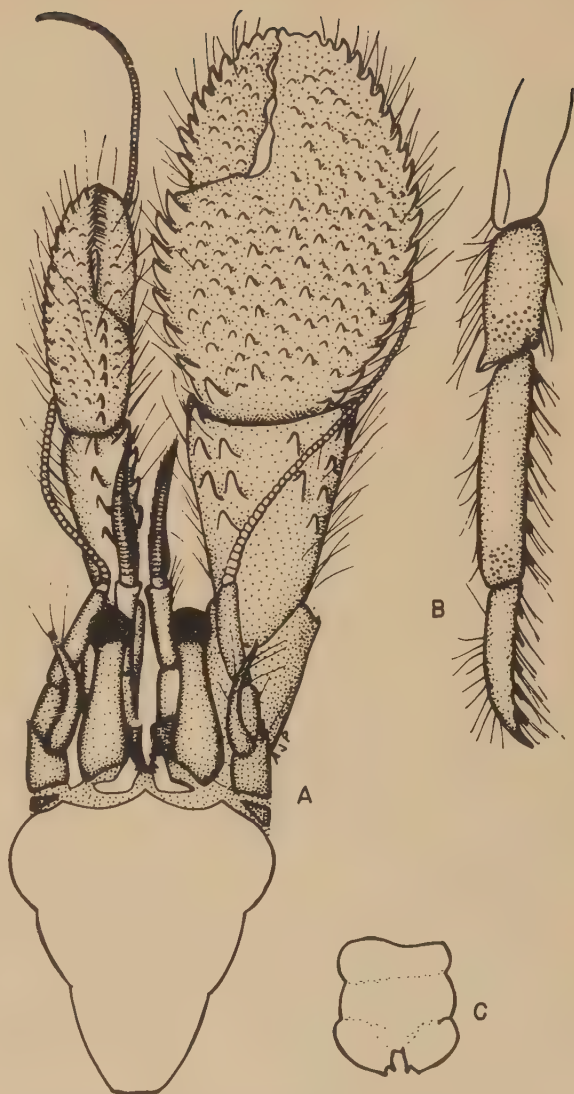


FIGURE 106.—*Pagurus pygmaeus* (Bouvier). A, anterior part of body and chelipeds in dorsal view; B, second left walking leg in lateral view; C, telson; A-C $\times 9$ (after Provenzano, 1959).

dactyls shorter than propodi, approximately five ventrally placed spines in addition to terminal point, propodus with about seven less conspicuous spines, all articles with long sparse setae.

Measurements.—Length of carapace: male, 3 mm.

Habitat.—Shallow water to 45 fathoms.

Type locality.—"La baie de la Zocappa," near Santiago, Cuba.

Known range.—Off Little River, South Carolina; southern Florida to Puerto Rico.

Remarks.—The occurrence of this species in the Carolinas is open to question because identification of the South Carolina material is not certain. Nevertheless, the species is included here. The South Carolina specimens were ovigerous females taken in August.

***Pagurus brevidactylus* (Stimpson)**

Figure 107

Eupagurus brevidactylus Stimpson, 1859, p. 91.

Pagurus brevidactylus: Provenzano, 1959, p. 413, fig. 20 (rev.).

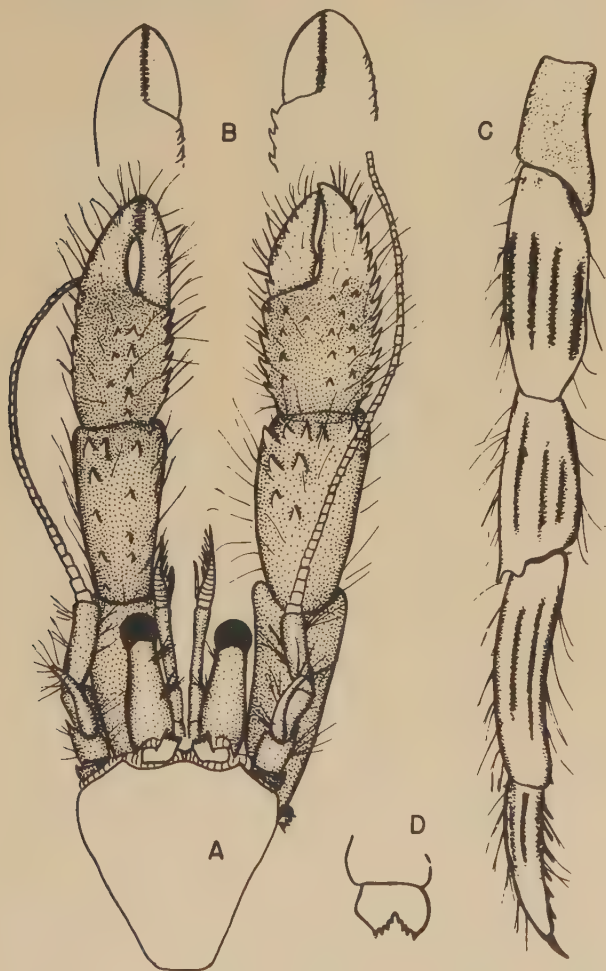


FIGURE 107.—*Pagurus brevidactylus* (Stimpson). A, anterior part of body and chelipeds, male in dorsal view; B, chelae of female in dorsal outline; C, second left walking leg in lateral view; D, telson; A–D approximately $\times 6$ (after Provenzano, 1959).

Recognition characters.—Anterior shield of carapace slightly longer than broad. Rostrum obsolete and about on line with triangular lateral

projections. Eyestalks swollen at base, tapering toward cornea; eye scales armed along anterior border with three to six spines. Antennular peduncles reaching at least to tips of eyestalks. Antennal peduncles slightly exceeding eyestalks; acicles reaching to base of cornea or slightly beyond.

Chelipeds unequal in males, right larger than left, equal or subequal in females; finger tips corneous, spooned. Hands covered with fine hairs, outer margin edged with spines, upper surface with smaller spines in several rows; carpi with strong spines above. Walking legs with long, fine, inconspicuous hairs; dactyls shorter than propodi and with five to eight conspicuous spines along inferior margin; propodi with only one or two inconspicuous spinules along inferior margin.

Measurements.—Length of carapace: male, 3 mm.; female, 4 mm.

Color.—Walking legs each characteristically colored with six rust-red, or maroon stripes on propodus, carpus, and merus, fewer on dactyl; stripes longitudinal and interrupted at ends of each article; ground color of walking legs yellow; hands brown with almost white fingers, not striped; carapace with scattering of red and white pigment in fresh specimens (Provenzano, 1959).

Habitat.—The species seems to prefer hard bottom in areas where water circulation is fairly good (Provenzano, 1959); has been taken from the Black Rocks in North Carolina; 1 to 125 fathoms.

Type locality.—Barbados.

Known range.—Off New River, N.C.; southwestern Florida from Anclote section southward; through West Indies to Barbados.

Remarks.—Provenzano (1959) called attention to the sexual dimorphism in this species. In females the hands are nearly the same size and the right hand is spooned and serrate along the inside margin of the fingers, whereas in males the right hand is not only the larger, but the finger tips appear more acuminate and the opposing margins of the fingers each bear a tooth. The specimens listed by Pearse and Williams (1951) as *P. bonairensis* are *P. brevidactylus* (U.S. National Museum notes).

Ovigerous females have been collected from June to August in North Carolina, March to August in Florida, and in April in Cuba.

Genus *Spiropagurus* Stimpson, 1858

Stimpson, 1858, p. 236.—Milne Edwards and Bouvier, 1893, p. 110.—Alcock, 1905, p. 117.

Spiropagurus dispar Stimpson

Figure 108

Spiropagurus dispar Stimpson, 1858, p. 236 [*nomen nudum*].—1859, p. 88.—Provenzano, 1961, p. 165.

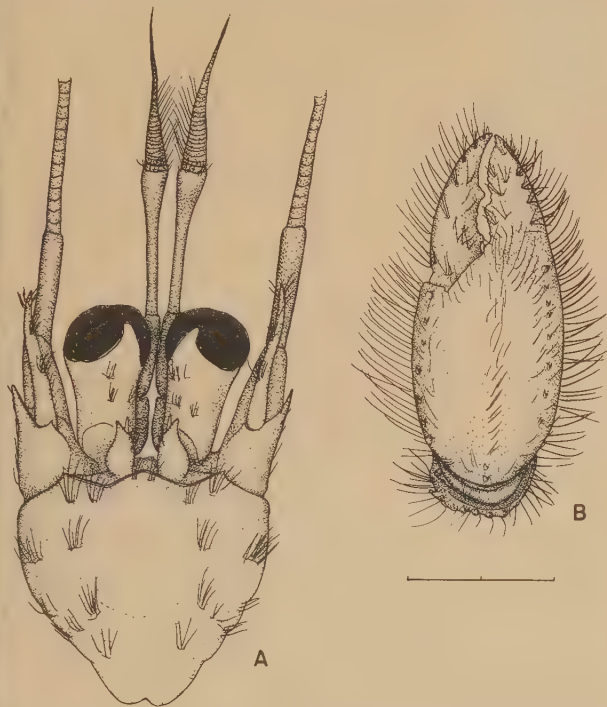


FIGURE 108.—*Spiropagurus dispar* Stimpson. A, anterior part of body in dorsal view; B, right chela, outer surface; 2 mm. indicated.

Recognition characters.—Carapace smooth but with hairy tracts on subcordate anterior shield and especially on anterior portion of membranous branchial areas; anterior margin with broadly rounded rostrum and equally advanced, acute lateral projections. Eyestalks more than twice as long as basal width, slightly exceeding proximal end of terminal articles of antennal and antennular peduncles, much dilated distally, cornea large; eye scales triangular, with abruptly narrowed acute tip directed slightly laterad, and slightly exceeded by strong subterminal spine. Acicles slender, longer than eyestalks.

Chelipeds elongate, setiferous, right chela larger than left. Major cheliped with fingers one-third to one-half length of palm, cutting edges of fingers toothed; palm ornamented with a dorsal,

submarginal row of distinct spines on each side; carpus shorter than palm with scattered spines dorsally; merus with a single spine on internal anterior border, and a short row of spines on corresponding external border. Minor cheliped similar but narrower; palm less spiny, and fingers with a row of fine denticles on opposed edges. Anterior two pairs of walking legs elongate, slender distally, somewhat less pubescent than chelipeds; dactyls not dilated noticeably at base; carpi with a low crest of spines.

Left vas deferens of male prominent and coiled in a loose spiral.

Measurements.—Length of carapace: male, 5 mm.

Color.—Anterior carapace with three pairs of pigment spots, anterolateral vertical flaps light brown with a large, clear or colorless spot; cornea deep brown, eyestalks brown dorsally and ringed with brown near base; a narrow brown-orange ring at middle of fingers and at edge of immovable finger, hands reticulated with brown on upper surface; walking legs with a broad brown band on dactyls; propodi with a dorsal and ventral brown patch, a faint longitudinal lateral stripe, and a pair of dorsomedial brown patches; carpi with three faint stripes laterally (Provenzano, 1961, from specimen preserved in formalin).

Habitat.—The species has been found housed in *Natica canrena* Linné; 5 to 100 fathoms.

Type locality.—Barbados.

Known range.—Off South Carolina; Virgin Islands; Barbados.

Remarks.—Ovigerous females have been taken from the Virgin Islands in April and September (Provenzano, 1961).

Genus *Pylopagurus* Milne Edwards and Bouvier, 1893

Milne Edwards and Bouvier, 1893, p. 74.

KEY TO SPECIES IN THE CAROLINAS

- a. Large chela almost smooth on upper surface, border finely crenulate; abdomen straight—*discoidalis* (p. 134).
- aa. Large chela more or less tuberculate on upper surface, border definitely toothed; abdomen coiled.
- b. Outer surface of chelae nearly flat, not conspicuously tuberculate; rostrum exceeding unarmed lateral projections of front—*corallinus* (p. 134).
- bb. Outer surface of chelae conspicuously convex, conspicuously tuberculate; rostrum about equal to prominent minutely armed lateral projections of front—*rosaceus* (p. 135).

Pylopagurus discoidalis (Milne Edwards)

Figure 109

Eupagurus discoidalis Milne Edwards, 1880, p. 41.
Pylopagurus discoidalis: Milne Edwards and Bouvier, 1893,
p. 76, pl. 6, figs. 7-14.

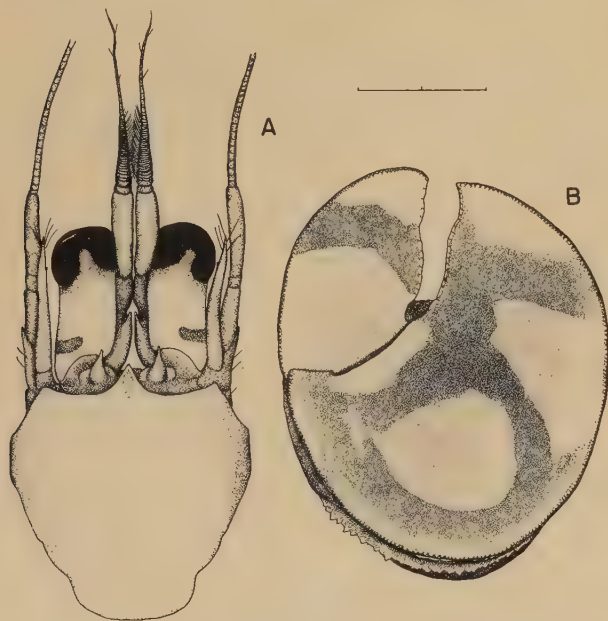


FIGURE 109.—*Pylopagurus discoidalis* (Milne Edwards).
A, anterior part of ovigerous female in dorsal view,
eyestalks showing color pattern; B, right (major) chela
of ovigerous female, upper surface showing color pat-
tern; 2 mm. indicated.

Recognition characters.—Anterior shield of carapace strongly calcified, subcordate, truncate posteriorly; anterior margin with large, sharp-pointed rostrum extending beyond middle of eye scales; lateral projections low and rounded, borders lateral to them very oblique. Eyestalks short, thick, widest distally, much shorter than length of frontal border, slightly exceeding acicles but not reaching middle of terminal article of antennular and antennal peduncles, cornea large; eye scales narrow, lanceolate. Acicles without spines and deflected somewhat outward.

Chelipeds unequal, right larger than left. Major chela in form of operculum adapted to close openings in *Dentalium* shells or similar tubes. Chela flexing at right angle on carpus and incapable of complete extension; upper surface smooth, flattened, or slightly excavated, nearly discoidal in outline, surrounded by a raised, finely crenulate

border; lower surface slightly wrinkled with lines; fingers compressed, internal border of dactyl with rounded tubercles; carpus short, dilated in front, external surface ornamented with granulations following feebly squamose, irregular lines (occurring also on hand, back of edge forming operculiform portion), and with a few denticles on anterior border. Minor cheliped shorter than right one; chela oval, with very fine denticles on external border; fingers agape at base, and terminating in corneous tips; carpus with some spines on crest. Walking legs reaching tip of major chela, dactyls lanceolate with corneous terminal claw well developed.

Measurements.—Length of carapace: male, 11 mm.; female, 10 mm.; sexual maturity attained at cephalothorax length of 4-5 mm.

Variations.—The large chelae become more discoidal with advancing age (Milne Edwards and Bouvier, 1893).

Color.—Whitish but with large areas of reddish on hands, on each article of legs, and a ring of same color near base of eye; reddish color may extend over anterior portion of cephalothorax (Milne Edwards and Bouvier, 1893).

Habitat.—The species has been taken from *Dentalium* shells and from annelid tubes of similar shape; 30 to 508 fathoms.

Type locality.—Montserrat, 120 fathoms.

Known range.—Off North Carolina capes, through eastern Gulf of Mexico and West Indies to mouth of Amazon River, Brazil (Provenzano, 1963).

Remarks.—Ovigerous females have been recorded in November from southern Florida and Brazil.

Pylopagurus corallinus (Benedict)

Figure 110

Eupagurus corallinus Benedict, 1892, p. 23.
Pagurus corallinus: Hay and Shore, 1918, p. 412, pl. 30, fig. 4.

Recognition characters.—Anterior shield of carapace subcordate, truncate posteriorly. Rostrum obtuse, produced beyond rounded, unarmed, lateral projections of front. Eyestalks stout, falling far short of tip of antennular peduncle, largest distally, cornea dilated; eye scales sharp pointed, and with a prominent subterminal spine. Antennal peduncle nearly as long as that of antennule; acicle reaching nearly to tip of cornea.

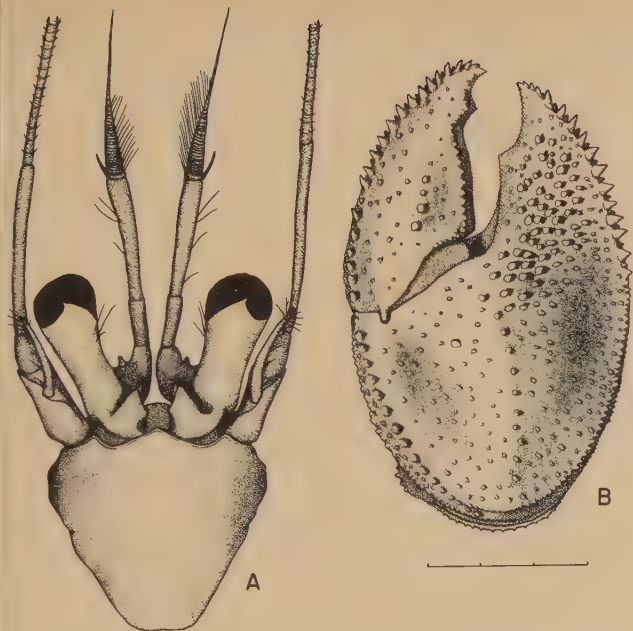


FIGURE 110.—*Pylopagurus corallinus* (Benedict). A, anterior part of body in dorsal view; B, right chela, outer surface; (from two specimens) 3 mm. indicated.

Chelipeds unequal, right larger than left. Upper surface of major chela flattened or slightly excavated, covered with small, slender spines becoming flattened and mushroom-shaped on immovable finger; hand fringed with spines, often alternately large and small, becoming longer near tips of fingers, inner surface with spinose tubercles between base of dactyl and recess receiving carpus, recess bounded by crest; carpus approximately as long as palm, upper surface thickly set with sharp, spiny granules, margin with rows of small spines; merus compressed, quadrilateral when viewed laterally. Minor chela with hand broad, compressed; fingers broad, gaping at base; carpus compressed, and surmounted by an inner row of small and an outer row of larger spines; merus compressed. Carpus and propodus of first walking leg, and carpus of second, crested with acute spines.

Measurements.—Length of carapace: male, 7 mm.; ovigerous female, 5 mm.

Color.—Large cheliped with merus and carpus blotched red and white; small cheliped and walking legs banded with same colors (Benedict, 1892).

Habitat.—In tunicates, stony corals, and bryozoans; 21 to 56 fathoms.

Type locality.—Off Key West, Fla.

Known range.—Off Cape Lookout, N.C., to Gulf of Mexico between Cedar Keys, Fla., and Mississippi Delta; off Cape Catoche, Yucatan, Mexico.

Remarks.—Ovigerous females have been taken off South Carolina in March, and southern Florida in June.

Pylopagurus rosaceus Milne Edwards and Bouvier

Figure 111

Pylopagurus rosaceus Milne Edwards and Bouvier, 1893, p. 97, pl. 7, figs. 10–17.—Hay and Shore, 1918, p. 413, pl. 30, fig. 5.

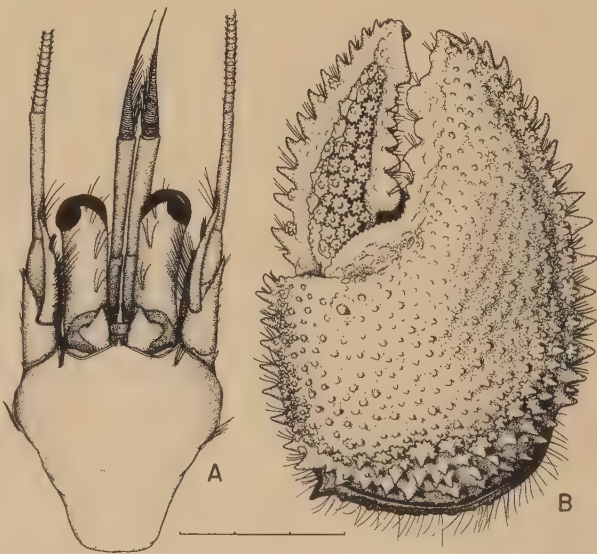


FIGURE 111.—*Pylopagurus rosaceus* Milne Edwards and Bouvier. A, anterior part of body in dorsal view; B, right chela, outer surface with detail shown only on dactyl; (from two specimens) 3 mm. indicated.

Recognition characters.—Anterior shield of carapace subcordate, somewhat truncate posteriorly; anterior margin with three projections, rostrum obtuse and slightly advanced beyond strong lateral projections, each terminating in a minute spine; sides of dorsal surface and anterior surface with a few tufts of setae. Eyestalks stout, considerably shorter than anterior shield, distinctly dilated distally, and with three or four pencils of setae in line along upper surface; eye scales acute anteriorly, each ending in an acute, subterminal spine. Antennal peduncle extending beyond eye, flagellum slender and longer than body; acicle strongly curved, reaching almost to distal edge of cornea.

Chelipeds unequal, right much larger than left. Both chelae capable of being bent down at a right angle to carpus to form, either singly or together, an operculum closing orifice of cavity inhabited by crab. Both margins of major chela, and outer margin of minor one, armed with a row of close-set, conical teeth; upper surface of both covered with closely crowded, rosettelike tubercles, each consisting of a central larger tubercle surrounded by a number of smaller ones; inner surface of major hand nearly smooth between base of dactyl and recess receiving carpus. Carpus of major cheliped with scattered sharp spines and hairs dorsally; merus with cross striae on upper surfaces and with anterior edges serrated with teeth in a single row. Minor cheliped similar but hairier and with a crest of spines on carpus. Walking legs of medium length, first and second of left side, and second of right side, exceeding large chela.

Measurements.—Length of carapace: male, 9 mm.; female, 10 mm.

Habitat.—The type was taken from an unknown species of the molluscan genus *Antillophos* (= *Phos*); 65 to 92 fathoms.

Type locality.—Grenada, 92 fathoms.

Known range.—South of Cape Lookout, N.C.; off Western Dry Rocks, Key West, Fla.; Grenada, and Surinam.

Remarks.—An ovigerous female has been taken from the Surinam locality in September.

Superfamily Hippidea

Abdomen reduced in size, bent under thorax; appendages of sixth segment not adapted for swimming. First pair of legs simple or subchelate, second to fourth legs with last article curved and flattened. Rostrum small or wanting. Third maxillipeds without epipodites.

Family Albuneidae

Carapace flattened and without wings covering legs. First pair of legs subchelate. Third maxillipeds narrow. Telson not conspicuously lengthened, almost oval.

KEY TO GENERA IN THE CAROLINAS

- a. Eyestalks narrow, triangular.....*Albunea* (p. 136).
 aa. Eyestalks broad, oval.....*Lepidopa* (p. 138).

Genus *Albunea* Fabricius, 1798

Gordon, 1938, p. 190.

KEY TO SPECIES IN THE CAROLINAS

- a. Dactyl of second and third legs with blunt, rectangular lobe at base of anterior border.....*gibbesii* (p. 136).
 aa. Dactyl of second legs with asymmetrically mucronate spur, and third legs with acute, falciform spur at base of anterior border.....*paretti* (p. 137).

Albunea gibbesii Stimpson

Figure 112

Albunea symniata Gibbs, 1850, p. 187.

Albunea gibbesii Stimpson, 1859, p. 78, pl. 1, fig. 6.—Benedict, 1901, p. 139.—1904, p. 625.—Hay and Shore, 1918, p. 414, pl. 30, fig. 11.—Schmitt, 1935a, p. 208.—Gordon, 1938, fig. 3e, p. 192, fig. 4b, p. 194.

Recognition characters.—Carapace about as broad as long, convex from side to side, nearly straight from front to back; front with a minute rostrum, and at either side a strong spine followed by 7 to 10 slender spines; anterolateral angle with a stout conical spine below *linea anomurica* projecting little if any beyond anterior border; posterior margin deeply and broadly notched; dorsal surface with numerous, irregular, more or less transverse, impressed lines, a short ciliated one near front, and one crossing near middle in shape of spread M being most conspicuous.

Eyestalks narrow, triangular, cornea at tip minute. Antennules about twice as long as carapace; flagella slender and densely ciliated above and below along inner surface, forming respiratory tube when approximated. Basal article of antenna with an acute, small, lateral spine; flagellum about half as long as peduncle. First pair of legs stout, hairy, all but distal articles inflated; hand subchelate; inferior distal angle of propodus produced into a spine; dactyls curved and rather slender. Second, third, and fourth legs stout, hairy, and with falcate dactyls; dactyl of third leg with falciform spur at base of anterior border, and second with similar broader spur. Fifth legs weak, borne above others.

Second, third, and fourth abdominal segments with expanded pleura, fifth and sixth segments small. Female with long uniramous pleopods on second to fifth segments. Uropods consisting of a rather large basal article and two small falcate blades. Telson of male triangular, of female rounded.

Measurements.—Length of carapace: male, 16 mm.; female, 20 mm.

Variations.—There is some individual variation in the pattern of spines on the anterior margin of the carapace. Spines may vary in number, be single, or occasionally be so close together as to appear doubled.

Color.—Light brown to orange tan above, cross striae lighter, with irregularly placed iridescent areas; antennules with alternating light and dark bands; eyestalks with a white ring behind cornea; underparts light (from recently preserved specimens). Light purple with whitish markings, more or less iridescent (various authors).

Habitat.—Sandy bottoms; extreme low-tide mark to 35 fathoms.

Type locality.—St. Augustine, Fla. (Stimpson); Sullivans Island, S.C. (Gibbes).

Known range.—East of Cape Lookout, N.C., to Texas; through West Indies to São Sebastião, São Paulo, Brazil.

Remarks.—*Albunea gibbesii* is occasionally found on sandy shoals, especially at times of extremely low tides when heat from the sun warms the exposed sand and drives the animals to the surface. Occasional specimens are found by digging, and specimens have been taken in both the Carolinas by dredging to depths of 35 fathoms.

Ovigerous females have been taken in North Carolina in June.

Pearse, Humm, and Wharton (1942) showed that *A. gibbesii* burrows backward into the sand as do the similar highly specialized sand dwellers, *Lepidopa websteri* and *Emerita talpoida*. These authors stated that *A. gibbesii* scrapes food from the setose antennules with the mouth parts; however, the chelate first legs and well-developed mandibles suggest feeding habits more like those of *Lepidopa* species. The function of the antennules as a possible feeding device was discussed by Benedict (1904).

Albunea paretii Guérin.

Figures 112–113

Albunea oxyophthalma Leach (MS) in White, 1847b, p. 57 (nomen nudum).

Albunea paretii Guérin, 1853, p. 48, pl. 1, figs. 10–10a.

Albunea paretot: Monod, 1956, p. 37, figs. 2–9 (rev.).

Recognition characters.—Similar to *A. gibbesii*, differing chiefly in characters given in key; dactyl of second legs with asymmetrically mucronate spur, third legs with acute, falciform spur at base of anterior border.



FIGURE 112.—Dactyls of second to fourth legs (from right to left); upper row, *Albunea paretii* Guérin; lower row, *Albunea gibbesii* Stimpson (after Gordon, 1938).



FIGURE 113.—*Albunea paretii* Guérin. Animal in dorsal view, legs of left side not shown, 5 mm. indicated.

Measurements.—Length of carapace: female, 20 mm.

Habitat.—Sandy bottom; low-tide mark to 21 fathoms.

Type locality.—[Uncertain], America.

Known range.—Beaufort Inlet, N.C., to Corpus Christi, Tex.; through West Indies to near mouth of Amazon River, Brazil; Bermuda; Cape Verde Islands and Senegal to Gold Coast, West Africa.

Remarks.—Monod (1956) reviewed the tangled history of the names given this species, but emended the specific name to conform to the name of the donor of the type specimen, Marquis of Pareto. Since Guérin used the spelling *paretii* twice in the original description, this spelling must be regarded not as a printer's error but as intentional (Holthuis, personal communication).

Ovigerous females have been taken in June in North Carolina.

Genus *Lepidopa* Stimpson, 1858

Stimpson, 1858, p. 230.—Holthuis, 1960a, p. 27 (rev.).

Lepidopa websteri Benedict

Figure 114

Lepidopa venusta: Kingsley, 1880, p. 410.

Lepidopa websteri Benedict, 1903, p. 892, fig. 3.—Hay and Shore, 1918, p. 415, pl. 30, fig. 12.



FIGURE 114.—*Lepidopa websteri* Benedict. Animal in dorsal view, first to fourth legs of left side not shown, 5 mm. indicated.

Recognition characters.—Carapace about as broad as long; front fringed with setae, produced into a short, triangular rostrum with acuminate tip, and to either side of it a broadly triangular lateral projection with acuminate tip slightly more advanced; margin between base of rostrum and each lateral projection almost straight; anterolateral angle produced into a flat spine above *linea anomurica*; sides sinuous and slightly convergent posteriorly, folded inward ventrally over bases of legs, more or less membranous posteriorly; dorsal surface crossed near front by an impressed, ciliate band with ends directed posteriorly, a narrower interrupted band ending in obliquely impressed lines crossing at about middle of carapace; posterior margin concave at middle.

Eyestalks irregularly oval, lamellate. Antennules with peduncles exceeding eyestalks; flagella straight, slender, nearly three times as long as carapace, fringed with hairs, and forming a respiratory tube when approximated. Antennae inserted at extreme outer angles of front, basal article stout; antennal scale reduced to a minute point; flagellum stout, curved, composed of seven short joints. First legs with broad, flat articles; dactyl turned back on propodus to form subchela. Second, third, and fourth legs with terminal joint bifurcated. Fifth legs much reduced, slender, and folded.

Abdomen short and partly flexed beneath thorax; second, third, and fourth segments with expanded pleura. Uropods small, with slender basal article, and long, oval blades, their margins and those of abdominal segments fringed with long, silky hairs. Telson cordate.

Measurements.—Length of carapace: 12 mm.

Color.—All parts white, iridescent, with pink being most conspicuous tint on anterior part of carapace, and blue showing along sides, in depressions of carapace, and on extremities of fifth legs; dorsal plates of abdomen faintly pink tinged, bordered by a delicate blue green; on either side of middorsal line, pink shading into red, and blue becoming deeper in shade (from note by A. Shaftsbury, U.S. National Museum records).

Habitat.—Usually found on gradually sloping sand beaches of open ocean at or immediately below low-tide mark (Pearse, Humm, and Wharton, 1942); shallow water, limits unknown.

Type locality.—Beach near Fort Macon, [Carteret County], N.C.

Known range.—Drum Inlet to Beaufort Inlet, N.C.; Ship Island and Petit Bois Island, Miss.

Remarks.—Knowledge of the ecology of this species is confined to the brief account given by Pearse, Humm, and Wharton (1942) which included detailed drawings of the specialized legs, as well as a lateral view of the whole animal. The species is highly adapted for burrowing in sand, and is usually found in small numbers. It burrows backward, and at rest lies at an angle to the surface with the long antennules extended in the water above. If disturbed, the animals may descend several centimeters into the sand. Benedict (1904) commented on the possible feeding function of the antennules in the genus *Lepidopa*. In 1903, he found setae of annelids, skin of a small *Synapta*, and parts of the flagella of some small crustaceans among stomach contents of *Lepidopa scutellata*. Such finding would be in accord with the fact that *Lepidopa*, like *Albunea*, has well-developed mandibles (Snodgrass, 1952).

Ovigerous females have been taken in July, and juveniles taken in plankton tows in July and August in North Carolina.

Family Hippidae

Carapace subcylindrical, and with wings covering legs. First legs simple. Third maxillipeds broad. Telson lengthened, lancet-shaped.

Genus *Emerita* Scopoli, 1777

Heegaard and Holthuis, 1960, p. 181.

KEY TO SPECIES IN THE CAROLINAS

(After Schmitt, 1935a)

- a. Dactyls of first legs subacute or sharply pointed distally; transverse rugosities more or less continuous over dorsum and continued posteriorly to inferior margin of carapace wings.....*benedicti* (p. 139).
- aa. Dactyls of first legs rounded or obtuse distally; lateral expansions or wings of carapace for greater part smooth and punctate.....*talpoida* (p. 140).

Emerita benedicti Schmitt

Figure 115

Emerita benedicti Schmitt, 1935a, p. 215, figs. 71 a, b.—Lunz, 1939, p. 336.

Recognition characters.—Body convex, oval; carapace firm; transverse rugosities more or less continuous, close set, and crossing whole of dor-

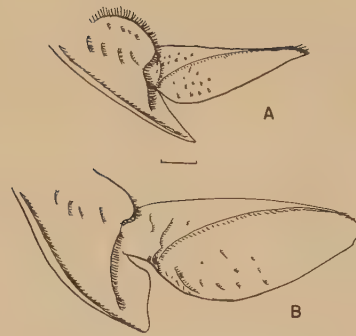


FIGURE 115.—Dactyl and portion of propodus of first leg; A, *Emerita benedicti* Schmitt; B, *Emerita talpoida* (Say); 1 mm. indicated.

sum, those on posterior part continued on wings of carapace to inferior margin. Rostrum equilaterally triangular in shape, separated by a rounded sinus on each side from a prominent and subacute tooth; an impressed, transverse line behind rostrum and a deeper, more strongly curved one farther back. Posterolateral margins extending downward to cover bases of legs; anterolateral margins concave and subserrate.

Eyestalks long, slender; cornea minute. Antennules about three times length of eyestalks; basal article with flagella hairy, forming respiratory tube when approximated. Antennae normally held beneath third maxillipeds, nearly twice as long as carapace when extended; first peduncular article short, second one largest, with outer margin produced into a strong superior, and much longer inferior, spine, both exceeding eyestalks; flagellum densely beset laterally with eight rows of fringed setae, outer rows longest.

First pair of legs directed forward, articles more or less hairy, and with impressed, interrupted, transverse ciliated lines; dactyl subacute distally; fifth article spinose distally. Second, third, and fourth legs less strong, hairy, tips curved and foliaceous. Fifth legs almost filamentous, entirely concealed beneath abdomen.

Abdomen broadest anteriorly, narrow posteriorly, flexed so that telson and sixth segment lie beneath body. Uropods turned forward, resting along sides of proximal segments. Telson elongate, lanceolate, margined with reflected setae above and inflected ones on edge; base with two short, impressed lines.

Measurements.—Length of carapace: ovigerous female, 18 mm.

Habitat.—Shell bottom, and probably other types (Lunz, 1939); to 2 fathoms.

Type locality.—Tampa Bay, Fla.

Known range.—Type locality, and Folly River to Edisto Island, Charleston County, S.C.; Gulf coast of Texas.

Remarks.—Lunz (1939) reported ovigerous females from South Carolina in June, and they are also known from there in July.

Emerita talpoida (Say). Mole crab; sand bug

Figures 115-116

Hippa talpoida Say, 1817, p. 160.

Hippa emerita: Ortmann, 1896 (in part), p. 232.

Emerita talpoida: Hay and Shore, 1918, p. 416, pl. 30, fig. 8.—Schmitt, 1935a, p. 216, figs. 74 a, b.—Snodgrass, 1952.

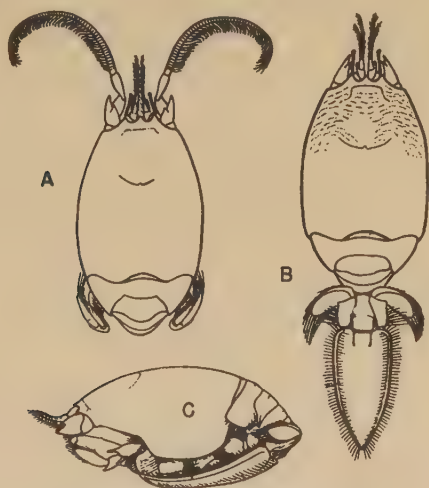


FIGURE 116.—*Emerita talpoida* (Say).
A, animal in dorsal view, antennae extended; B, animal in dorsal view, abdomen extended; C, animal in lateral view (after Snodgrass, 1952).

Recognition characters.—Body convex, oval; carapace firm, with overlapping rugosities anteriorly, smoother and polished posteriorly. Anterior margin with a small, blunt rostrum separated by a rounded sinus on each side from a more prominent and acute tooth; an impressed, transverse line behind rostrum, and a deeper, more strongly curved one farther back. Posterolateral margins extending downward to cover bases of legs; anterolateral margins concave and subserrate.

Eyestalks long, slender; cornea minute. Antennules approximately twice length of eyestalks;

basal article with a strong, external spine; flagella hairy, forming respiratory tube when approximated. Antennae, normally held concealed beneath third maxillipeds, nearly twice as long as carapace when extended; first peduncular article short, second one largest with outer margin produced into a strong, anteriorly directed spine widely bifid at tip with a deep fissure below; flagellum densely beset laterally with eight rows of fringed setae, outer rows longest. First pair of legs directed forward, articles more or less hairy, and with impressed, interrupted, transverse ciliated lines; dactyl rounded distally, fifth article spinose distally. Second, third, and fourth legs less strong, hairy, tips curved and foliaceous. Fifth legs almost filamentous, entirely concealed beneath abdomen.

Abdomen broadest anteriorly, narrow posteriorly; flexed so that telson and sixth segment lie beneath body. Uropods turned forward, resting along sides of proximal segments. Telson elongate, lanceolate, margined with reflected setae above and inflected ones on edge; base with two short, impressed lines.

Measurements.—Length of carapace: males, 11 mm.; females, 26 mm.

Color.—Uniform pale yellowish brown (Snodgrass, 1952).

Habitat.—Sandy beaches in and below surfline; to 2 fathoms in winter.

Type locality.—[East] coast of United States.

Known range.—Harwich, [Barnstable County], Mass., to east coast of Florida; west coast of Florida to Grand Isle, La.; Progreso, Yucatan, Mexico (Schmitt, 1935a).

Remarks.—The general ecology of *Emerita talpoida* as a representative of the specialized sandy-beach fauna has been studied by a number of workers, especially Wharton (1942). The eggs are bright orange when first laid and gradually fade to a translucent dirty gray just before hatching. Wharton gave a figure of the mature sperm cell, and Herrick (1892, pl. 25) gave figures of developmental stages in the egg. Wharton found the breeding season in North Carolina to extend from early June through September, and Fish (1925) found larvae at Woods Hole, Mass., from late July to early September. In Florida, ovigerous females have been found in November. The larval stages were most completely described by

Rees (1959) from rearing experiments in the laboratory. Larval development lasts 28 days and normally encompasses at least six zoeal stages. Rees also described the megalops stage which resembles the adult in shape.

Wharton found megalops in large numbers in sand washed by waves. This stage swims with the abdomen extended, whereas young adults swim with the abdomen flexed. Megalops and young adults were found to be distributed evenly in the wave-washed zone rather than in colonies as are adults. Wharton traced development of the pleopods of females from the truly swimming appendages of the megalops to the uniramous non-swimming pleopods of adults. Adult males lack pleopods.

The average carapace length of young adult females increased from 3 mm. in early summer to 8 mm. the following May, and by August had increased to 18 mm. (maximum, 26 mm.). Wharton thought that females have one reproductive period in summer at an age of about 1 year, then live a short time longer and die at an age of about 1 year and 3 months. Williams (1947), studying size-frequency distributions, thought that they live to be 2 years of age, and Edwards and Irving (1943) stated that at Woods Hole females live 27 months, males 25. Since large females (to 21 mm.) can be taken in winter, the latter estimates are more likely correct, and Wharton's 26-mm. female was probably 2 years old.

Small males appear about the same time as females. Sexually mature at very small sizes (carapace length, 3 mm.) they seek out and attach themselves to year-old females. As many as seven small males were found on a single large female, and Wharton judged that they remain attached for long periods:

The attachment of the small males to the large females is achieved by various methods. These semiparasitic mates have been found in the gill chambers, clamped between the coxae of the thoracic appendages, attached to egg masses, clamped by means of their telson to the ovigerous hairs of the pleopods, and some seen to roam about on the ventral surface of the larger females. A few males seemed to be attached by means of the spermatophores which are extruded from the basal segment of the fifth leg; however, these may have been merely depositing the spermatophores.

By winter, the males are free living, and by the following June attain a size of about 7 mm. (max-

imum, 10 mm.). Wharton thought that these die in July after a possible second mating period.

It was estimated that growth of large females from early June to late August may be as much as 0.08 mm. per day. However, both Wharton (1942) and Williams (1947) noticed that there is considerable annual fluctuation in size at the same locality, and Williams further stated that there is considerable variation in size between localities in the same year.

The beautiful adaptations of this species for life in the shifting sand of the surf zone were treated by Wharton, and the anatomical specializations were exhaustively discussed by Snodgrass (1952). Adults can swim by means of the uropods, but they are primarily adapted for burrowing backward into wet sand. This is accomplished by rotating the uropods in unison, throwing sand dorsally, moving the second, third, and fourth legs laterally and posteriorly in unison, and by pushing the first legs alternately laterally and anteriorly. Once the animal is buried, the fringed antennae are allowed to lie on the sand extended anterolaterally to strain the receding water of waves. Stomach contents consist of small particulate matter, but the exact method of transfer of food from the antennae to the mouth is unknown.

Emerita talpoida moves up and down the beach with the tide, following shallow waves toward the water or moving up the beach with deep waves. Jones (1936) compared the habits of *E. emerita* to those of *E. talpoida* and devised a clever method of marking animals with string for the purpose of tracing their movements on the beach.

Edwards and Irving (1943) studied the influence of temperature and season on oxygen consumption in *E. talpoida* at Woods Hole. They found that oxygen consumption of winter animals at 12° C. is about the same as that of the smallest summer animals at 17° C.; consumption of winter animals at 3° C. is about the same as that of summer animals at 13° C. They concluded that *E. talpoida* from the Woods Hole area becomes adjusted to seasonal changes in temperature in such a manner that rate of metabolism in winter is kept at a level comparable to that in summer. This explains why growth is uniform throughout the year, though the animals live in 6 to 12 feet of water in winter rather than in the surf. The method of feeding in winter was not discussed.

Section Brachyura

Crabs with abdomen much reduced in size, straight, symmetrical, closely bent under thorax, never used for swimming, and with uropods rarely present, never biramous. Cephalothorax depressed, fused with epistome at sides and nearly always in middle. Antennal scales immovable. Third maxillipeds broad. First pair of legs chelate and nearly always much stronger than other legs.

Subsection Gymnopleura

Anterior thoracic sterna broad, posterior thoracic sterna narrow and keellike. Posterior thoracic epimera largely exposed by reduction of branchiostegite. Female openings on coxae. Last pair of legs dorsal in position, normal or reduced in size. Sternal canal present. Thoracic nerve ganglion-chain elongate. Antennary sternum triangular, spout-shaped. Branchiae eight on each side (Bourne, 1922).

Family Raninidae

Crabs with carapace remarkably elongate but not covering abdominal terga, first four or five terga lying exposed in dorsal plane of body. Last pair of legs also raised in dorsal plane of body. Antennae and antennules large, not folding into fossettes. Vasa deferentia protruding through bases of fifth pair of legs; oviducts piercing coxa of third pair of legs. Sternum broad anteriorly, narrow or linear posteriorly. A pair of respiratory orifices between tergum of first abdominal segment and coxae of last pair of legs. External maxillipeds completely covering buccal cavity, with palp concealed in repose; exopodite but little longer than ischium. Gills less than nine in number on either side. Hand flat, immovable finger extremely bent allowing movable finger to close against anterior border of hand. (Modified after Alcock, 1896, and Rathbun, 1937.)

Genus *Ranilia* H. Milne Edwards, 1837

Rathbun, 1937, p. 17.

Ranilia muricata H. Milne Edwards

Figure 117

Ranilia muricata H. Milne Edwards, 1837, p. 196.—Hay and Shore, 1918, p. 420, pl. 31, fig. 1.—Rathbun, 1937, p. 18, pl. 3, figs. 3-6; pl. 4, figs. 1-4 (rev.).

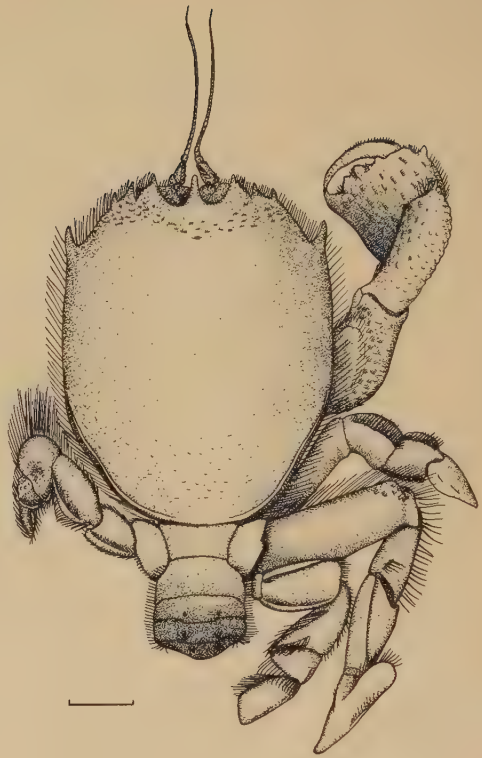


FIGURE 117.—*Ranilia muricata* H. Milne Edwards. Ovigerous female in dorsal view, first to fourth legs of right side shown, only fifth leg of left side shown, 5 mm. indicated.

Recognition characters.—Carapace oval, strongly convex from side to side, slightly so from front to back, smooth posteriorly but with numerous transverse ciliated wrinkles anteriorly. Rostrum slender; anterior border of carapace with four strong spines on each side, innermost overhanging base of orbit, third surmounting external angle of orbit, fourth at external angle of front. Eyestalks strong, about four times as long as rostrum, and capable of being turned back into deep, oblique orbits. Antennules small. Antennae directed forward, slightly longer than eyestalks.

First pair of legs subchelate, stout, flattened distally, squamous-denticulate above, with a strong spine on superodistal margin of merus, carpus, and hand; distal margin of hand perpendicular, toothed; dactyl strong, curved. Second, third, and fourth pairs of legs with flattened, triangular dactyls. Fifth pair of legs elevated, turned forward, fringed with hairs.

Abdomen short and narrow.

Measurements.—Carapace: length, 39 mm.; width, 28 mm.

Color.—Porcelain white with red, vermiculate, transverse lines on cephalothorax, and red dots and blotches on legs. Gibbes, in Rathbun (1937) gave the color of dry specimens as purplish mixed with yellow and orange in places, particularly about the articulations and spines, with the latter having white tips, and the chelipeds, walking legs, and abdominal segments with purplish markings.

Habitat.—This species appears to be confined to sand bottoms well offshore. Specimens have been obtained in dredge hauls, and fragments of others taken from fish stomachs off North Carolina. The species has not been found within Beaufort, N.C., harbor, nor along the beaches; 7 to 56 fathoms.

Type locality.—Unknown.

Known range.—Off Cape Lookout, N.C., to northwest Florida; Bahamas; Swan Island in Caribbean Sea.

Remarks.—Though this modern species has no fossil record in North America, the Family Raninidae in this region has a fossil record dating from the Cretaceous (Rathbun, 1935).

Rathbun (1937) reported ovigerous females in April from Florida, and in September from North Carolina.

Subsection **Dromiacea**

Carapace subglobose or subquadrate, frontal region narrow. Last one or two pairs of legs small, subdorsal in position. Abdomen folded under thorax, penultimate segment usually without appendages; five pairs of appendages in female, first pair rudimentary. Lateral thoracic apodemata united in common center, forming a sternal canal. External maxillipeds with merus and ischium subquadrate (Rathbun, 1937).

Family **Dromiidae**

Carapace subglobular, rarely flattened; no *lineae anomuricae* (a pair of longitudinal suture lines on carapace). Sternum of female traversed at least in part by two obliquely longitudinal grooves. External maxillipeds generally operculiform. Legs of moderate size; fourth and fifth pairs short, subdorsal in position, furnished with small hooklike nail or dactyl. Sixth segment of

abdomen generally with rudimentary uropods (Schmitt, 1921).

The significance of the obliquely longitudinal sternal grooves on the females of this family has recently been treated by Gordon (1950). She found these to be external evidence of a pair of involuted tubes (variously developed in different species) leading from an external opening at the anterior end of the grooves posteriorly to paired spermathecae enclosed in the endophragmal system.

The North American fossil record for this family dates from the lower Cretaceous of Texas (Rathbun, 1935), though no modern species in the Carolinian fauna possesses a known fossil record.

KEY TO GENERA IN THE CAROLINAS

- a. Carapace firm and hard; body covered with short pubescence-----*Dromidia* (p. 143).
- aa. Carapace soft and membranous; body mostly naked
Hypoconcha (p. 144).

Genus **Dromidia** Stimpson, 1858

Rathbun, 1937, p. 32.

Dromidia antillensis Stimpson

Figure 118

Dromidia antillensis Stimpson, 1859, p. 71.—Hay and Shore, 1918, p. 417, pl. 31, fig. 5.—Rathbun, 1937, p. 33, text-fig. 12, pl. 7, figs. 1-3 (rev.).

Recognition characters.—Body and legs covered with thick coat of short pubescence, leaving only parts of fingers exposed. Carapace convex in all directions, longer than broad; frontal region longitudinally grooved along middle; front strongly deflexed, with five small, slender teeth, median three subequal and approximately as long as distance between them at bases, teeth over eyes somewhat shorter but acute. Anterolateral margin of carapace deflected toward corner of buccal area, armed with four or five teeth.

Chelipeds rather thick and heavy; carpus dentate with small teeth at anterior angles; palm shorter than dactyl and armed with three blunt spines on upper margin; fingers curved, with strongly interlocking teeth. Walking legs rather slender; last pair turned forward over back, and much longer than fourth pair; dactyls of fourth and fifth legs hooked, closing against unequal pair of distal spines on propodus.

Measurements.—Carapace of male: length, 32 mm.; width, 31 mm.



FIGURE 118.—*Dromidia antillensis* Stimpson. Male in dorsal view, legs of left side not shown, 10 mm. indicated.

Color.—Quite variable. General ground color dirty yellowish green, olive buff, white, coral-mud gray, orange buff or various shades of red with lighter pubescence; fingers with bases darker than white tips, shades of orange, pink, or red; cornea of eyes gray, hazel, reddish speckled or brown; some specimens with bluish cast on maxillipeds and antennular peduncles. Rathbun (1937) gave great detail on a number of individuals which appeared to vary from light to dark in a harmonious set of colors.

Habitat.—Shore to 170 fathoms.

Type localities.—St. Thomas, V.I., Key Biscayne and Tortugas, Fla.

Known range.—Off Cape Hatteras, N.C., through Gulf of Mexico and West Indies, to State of Bahia, Brazil; Bermuda.

Remarks.—This species is usually found carrying a covering of compound ascidians, sponge, or zoanthoid polyps. The species is primarily southern in distribution, the North Carolina records representing marginal occurrence in a favorable northern locality. Hildebrand (1955) found it

common on the Campeche Banks shrimp grounds.

Rathbun (1937) reported ovigerous females from Florida and the West Indies in winter, spring, and summer.

Genus *Hypoconcha* Guérin, 1854

Rathbun, 1937, p. 44.

KEY TO SPECIES IN THE CAROLINAS

- a. Anterior margin of carapace without spines *arcuata* (p. 144).
- aa. Anterior margin of carapace with several strong spines *sabulosa* (p. 145).

Hypoconcha arcuata Stimpson

Figure 119

Hypoconcha arcuata Stimpson, 1858, p. 226.—Hay and Shore, 1918, p. 418, pl. 31, fig. 2.—Rathbun, 1937, p. 47, pl. 11, figs. 1–4.

Recognition characters.—Body short, broad, flattened, with a thin, parchmentlike covering dorsally, solid and roughly granulate ventrally. Appendages capable of being folded compactly against body. Front margin of carapace nearly semicircular in outline, margin densely ciliated, deeply fissured in middle and with a shallow notch on each side near middle. Ventral surface without ridges, sloping evenly to anterior margin, and with eyes, antennules, antennae, and mouth parts deeply seated in depressions; a narrow fissure in front of eye for lodgment of antennal flagellum; outer posterior margin of orbit fissured. Third maxillipeds completely closing buccal cavity.



FIGURE 119.—*Hypoconcha arcuata* Stimpson. Anterior portion of animal in ventral view, 3 mm. indicated.

Legs all stout, hairy, and coarsely granulate. First pair chelate; fingers somewhat spatulate and toothed at tip, immovable finger articulated at angle with hand. Second and third legs with sharp, corneous tips; fourth and fifth legs borne on dorsal surface, with penultimate article quite short, and terminal article reduced to a small, curved claw. Abdomen short and flexed so that last two segments lie on thoracic sterna.

Measurements.—Carapace of male: length, 24 mm.; width, 24 mm.

Color.—Gray.

Habitat.—This curious crab has been taken from dredge hauls in Bogue Sound off Morehead City, N.C. It is always found occupying a valve of some lamellibranch shell, preferably a clam-shell, which it carries about upon its back after the manner of a hermit crab. By means of the claws on its fourth and fifth pairs of legs, perhaps aided by pressure of its body against the shell, it clings so tightly that removing it from the shell without crushing it is almost impossible. Shallow water to 22 fathoms.

Type localities.—South Carolina sandy shores, and St. Thomas, [V.I.].

Known range.—Off Cape Lookout, N.C., to west Florida; St. Thomas, V.I.; Surinam to State of Espirito Santo, Brazil.

Hypoconcha sabulosa (Herbst)

Figure 120

Cancer sabulosa Herbst, 1799, p. 57, pl. 48, figs. 2-3.

Hypoconcha sabulosa: Hay and Shore, 1918, p. 418, pl. 31, fig. 3.—Rathbun, 1937, p. 44, pl. 8, figs. 3-4, pl. 9, figs. 1-5 (rev.).

Recognition characters.—Body short, broad, flattened, with front and lateral margin expanded, with thin parchmentlike covering dorsally, solid with surface nodulose, granulate, and marked by several strong ridges ventrally. Carapace in old individuals pubescent above; margin densely hairy, and armed anteriorly with four curved spines with sharp tips pointing obliquely downward followed by a few other smaller spines; front between median pair of spines subtruncate or sloping slightly backward toward short, narrow, median fissure. Antennal fossae limited in front by a pair of strong, oblique ridges arising between two of spines of anterior border, meeting each other in midline in front of epistome; epistome with posterior border raised into a promi-



FIGURE 120.—*Hypoconcha sabulosa* (Herbst). Anterior portion of animal in ventral view, detail of right side shown, 5 mm. indicated.

nent ridge continuing on either side across front and some distance along sides of buccal area. Basal articles of antennae tuberculate; proximal article with a strong inwardly directed tooth, distal article with a tooth on each side of base of flagellum. Fissure in outer margin of orbit prominent owing to development of a strong tubercle on either side.

Carpal article of first pair of legs with several dentate tubercles; hand covered with more or less pointed tubercles. Other legs and abdomen much as in *H. arcuata*.

Measurements.—Carapace of female: length, 22 mm.; width, 22 mm.

Color.—Gray; or, as described by Schmitt in Rathbun (1937), coral sand above with whitish-gray hairs, ground color beneath, red; rounded bosses on legs and subfrontal region reddish brown; eyes black or reddish brown; eggs orange.

Habitat.—A few feet to 49 fathoms.

Type locality.—Listed as "Africa" (probably an error).

Known range.—Off Cape Hatteras, N.C., to Sabine, Tex.; Jamaica.

Remarks.—This species has been found in Beaufort, N.C., harbor, and, though it apparently has habits similar to those of *H. arcuata*, it is much the rarer of the two species. Rathbun (1937) listed ovigerous females in June from Florida and in October from North Carolina.

Family Homolidae

Crabs with carapace rectangular, ovoid, or urn-shaped, longer than broad. Eyes incompletely sheltered by orbits when retracted, terminal joint of eyestalk either longer or shorter than slender basal joint. External maxillipeds pediform, subpediform, or suboperculiform. Sternum of female without longitudinal grooves. Gills 8, 10, 13, or 14 on each side (Rathbun, 1937, modified after Gordon, 1950; Hemming, 1958c).

Genus *Homola* Leach, 1815

Rathbun, 1937, p. 62.—Hemming, 1958c.

Homola barbata (Fabricius)

Figure 121

Cancer barbatus Fabricius, 1793, p. 460.

Homola barbata: Hay and Shore, 1918, p. 419, pl. 30, fig. 10.

Thelziope barbata: Rathbun, 1937, p. 63, text-fig. 16, pl. 15, figs. 1-2 (rev.).



FIGURE 121.—*Homola barbata* (Fabricius). Animal in dorsal view (after Smith, 1887).

Recognition characters.—Carapace about one-fourth longer than wide with surface granulate, spinulose, and sparsely setose; *linea anomurica* distinct and dorsal; sides nearly straight, only slightly convergent posteriorly, and extending almost vertically downward from a spiny ridge running backward from behind a strong spine situated at extremities of suture separating gastric and hepatic regions. Rostrum small, bifurcate at tip; a spine on each side at base of rostrum, one at

outer orbital angle, a transverse row of two behind rostrum, behind these a transverse row of eight, and farther back a small median spine. Anterolateral parts below and behind orbits with small spines. Eyestalks long, slender at base, and abruptly enlarged below cornea.

Chelipeds of moderate size, surface granulate and hairy; merus and carpus with rows of spines. Walking legs with flattened articles, long, hairy, and spinulose along margins. Second segment of abdomen with a large, median, conical tooth.

Measurements.—Carapace including rostrum: male, length, 30 mm., width at base of lateral spines, 22 mm., posterior width, 16 mm.; female, length, 33 mm., width at spines, 25 mm., posterior width, 20 mm.

Color.—"Body covered with tawny or yellowish-brown or reddish-brown hair; spines red or partly red" (Rathbun, 1937).

Habitat.—Thirty to 373 fathoms.

Type locality.—Bay of Naples.

Known range.—Off southeastern Massachusetts to Caribbean Sea; eastern Atlantic Ocean from Portugal and Azores to Madeira Islands; Mediterranean Sea; South Africa.

Remarks.—This essentially deep-water species has been reported in 63 fathoms off North Carolina. Ovigerous females have been reported in October off Delaware Bay (Rathbun, 1937), and are known off North Carolina and Florida in June and July.

Gordon (1950) discussed the anatomical structure of the spermathecae of females and copulatory apparatus of males in the genus *Homola*, and remarked upon the evolutionary sequence shown by these structures in the Dromiacea.

Subsection *Oxystomata*

Epistome reduced or absent. Efferent branchial channels terminating at middle of buccal area, buccal cavern produced forward and generally elongate-triangular in shape, efferent channels enclosed by an elongate lamellar process of exopods of first maxillipeds. Afferent branchial openings either in front of bases of chelipeds, or at sides of endostome. Gills six to nine on each side. Antennules folding either longitudinally or obliquely, rarely transversely. Male genital ducts protruding through bases of fifth legs or through

fifth thoracic sternum nearby. (Modified after Alcock, 1896, *in* Rathbun, 1937.)

Family Leucosiidae

Crabs having carapace circular, oval, or polygonal. Eyes and orbits small, front narrow but wider than orbit. Antennules folding more or less obliquely. Antennae small. External maxillipeds completely enclosing buccal cavity, except often a small crevice in front. Afferent branchial channels occupying sides of endostome on either side of deep, median, endostomal groove serving as an efferent branchial channel. Afferent channels covered by exognaths of external (third) maxillipeds, efferent channels by a pair of lamellar processes of first maxillipeds. Chelipeds symmetrical. Abdomen hidden beneath thorax, commonly with third to sixth abdominal terga fused, sixth sometimes free. Vasa deferentia opening on fifth thoracic sternum near bases of last pair of legs. (Modified after Alcock, 1896, *in* Rathbun, 1937.)

KEY TO GENERA AND SOME SPECIES IN THE CAROLINAS

- a. Carapace polygonal, uneven, nodular, or eroded
 - Subfamily Eballiinae (p. 147).
 - b. Posterior portion of carapace without deep cavities
 - Eballia cariosa* (p. 147).
 - bb. Posterior portion of carapace with a deep rounded cavity on each side-----*Speloeophorus* (p. 148).
- aa. Carapace ovoid or globular, and smooth or granular
 - Subfamily Philyrinae (p. 150).
 - b. Fingers opening in horizontal plane
 - Persephona punctata aquilonaris* (p. 150).
 - bb. Fingers opening in vertical plane
 - Iliacantha* (p. 150).

Subfamily Eballiinae

Surface of carapace uneven. Chelipeds of moderate length; fingers not very thin and elongate, dactyl moving in an oblique plane. Anterior margin of buccal cavity arcuate, middle part in front of level of anterior pterygostomian region. Epistome and infraorbital lobe well developed. Pterygostomian margin extending either slightly or distinctly forward, terminating in an indentation. Merus of external maxillipeds half or more than half length of ischium measured along inner border. First abdominal segment in female often under carapace (Rathbun, 1937).

Genus *Eballia* Leach, [1817]

Rathbun, 1937, p. 123.—Hemming, 1958b, p. 15.

Eballia cariosa (Stimpson)

Figure 122

Lithadia cariosa Stimpson, 1860a, p. 238.—Hay and Shore, 1918, p. 424, pl. 32, fig. 6.

Eballia cariosa: Rathbun, 1937, p. 125, pl. 35, figs. 6-7 (rev.).



FIGURE 122.—*Eballia cariosa* (Stimpson). Animal in dorsal view, legs of left side not shown, 3 mm. indicated.

Recognition characters.—Carapace convex, roughly pentagonal; anterior angle truncate, lateral angles obtuse; surface uneven and covered everywhere, including other parts of body and legs, with beadlike granules, larger posteriorly and ventrally. Front narrow, upturned, and broadly notched, connected with middle protuberances by a median ridge traversing gastric region; ridge flanked on each side by a sinuous, deep, broad excavation of darker color than protuberant parts. Anterolateral margin of hepatic region sinuous, hepatic region slightly prominent, delimited posteriorly by an impressed line. Pterygostomian region with a large downward-pointing tooth, hardly visible in dorsal view. Posterolateral margin with a broad tooth, separated from bilobate intestinal region by a deep sinus; cardiac and inner lobules of branchial region strongly protuberant, separated from thick intestinal lobes by a deep narrow sulcus.

Chelipeds stout, a little longer than width of carapace, joints angular; merus as broad as hand, outer margin convex and a little irregular; hands rather small, tapering to rather slender fingers. Walking legs cylindrical. Abdomen of male narrow, triangular, with a backward projecting spine at proximal end of penultimate segment. Abdomen of female with penultimate segment very large, nearly circular.

Measurements.—Carapace: length of male, 12 mm., width, 13 mm.; female, length, 13 mm., width, 15 mm.

Color.—Light gray or buff, female occasionally with two or three small red spots on abdomen; other specimens may be pale red (Rathbun, 1937).

Habitat.—Below low-tide mark to 25 fathoms.

Type locality.—Beaufort, N.C.

Known range.—Bogue Sound near Beaufort, N.C., to west Florida; Jamaica; northeastern South America to Rio de Janeiro, Brazil.

Remarks.—This species is occasionally found in channels in the Beaufort, N.C., harbor. The species feigns death when brought on deck in a dredge haul, and, thus, closely resembles the pebbles and pieces of shell among which it appears to live. Ovigerous females are found at this locality throughout the summer.

Genus *Speloeophorus* Milne Edwards, 1865

Rathbun, 1937, p. 141.

KEY TO SPECIES IN THE CAROLINAS

- a. Lateral portions of carapace tumid, not expanded into wings; deep cavity of carapace with only two openings, not visible dorsally.....*nodosus* (p. 149).
- aa. Lateral portions of carapace expanded into broad, flattened wings; deep cavity of carapace with four openings, two visible dorsally.....*pontifer* (p. 149).

Speloeophorus nodosus (Bell)

Figures 123-124

Oreophorus nodosus Bell, 1855, p. 307, pl. 33, fig. 8.

Speloeophorus nodosus: Hay and Shore, 1918, p. 425, pl. 32, fig. 5.—Rathbun, 1937, p. 142, pl. 40, figs. 1-5.

Recognition characters.—Carapace convex, roughly pentagonal or hexagonal, broader than long, posterolateral angles rounded; surface nodose, evenly and thickly covered everywhere with crowded, rounded granules. Front thick, bilobed, upturned; a prominent broad ridge extending backward from front to cardiac region. Hepatic region to each side with a low hump, behind this,



FIGURE 123.—*Speloeophorus nodosus* (Bell). Animal in dorsal view, legs of left side not shown, 3 mm. indicated.

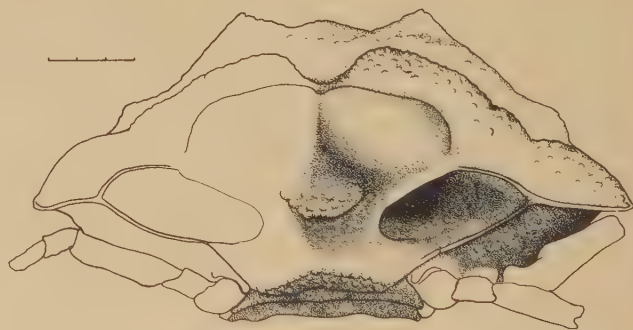


FIGURE 124.—*Speloeophorus nodosus* (Bell). Animal in posterior view, 3 mm. indicated.

at side of gastric region, a much larger hump, and still farther back, near posterior border, another of nearly equal size; posterior humps overhanging and largely containing a deep cavity with two openings invisible in dorsal view. Subhepatic region with a nodose prominence near front, and farther back two others of smaller size.

Chelipeds short, stout, coarsely granulate, crested along outer margin; merus with large distal and small proximal lobe; fingers thin, flat, grooved. Walking legs crested, crests dentate or narrowly lobed.

Measurements.—Carapace: length of male, 12 mm., width, 15 mm.; female, length, 17 mm., width, 21 mm.

Variations.—Carapace of males much more uneven than that of females.

Color.—Pink with a few purplish spots on carapace and rusty-brown marks on legs. Rathbun (1937) described this species as looking like a dead piece of coral overgrown with purplish and greenish algae, with patches of red ones; chelae with natural greenish cast; reticulations around whitish areas of green hue; fingers dull white with articulations pink; legs dirty white with greenish, reddish, and whitish spots; eyes not distinguishable from rest of body; underparts dirty white, abdomen greenish.

Habitat.—One and one-half to 10 fathoms.

Type locality.—Unknown.

Known range.—Off Morehead City, N.C., to southern Florida; West Indies.

Remarks.—This species is rare in the northern part of its range and was most recently reported by Pearse and Williams (1951) from reefs off Beaufort Inlet, N.C. The species readily plays dead when brought on deck.

***Speloeophorus pontifer* (Stimpson)**

Figures 125-126

Lithadia pontifera Stimpson, 1871b, p. 115.

Speloeophorus pontifera: Hay and Shore, 1918, p. 425, pl. 32, fig. 5.

Speloeophorus pontifer: Rathbun, 1937, p. 144, pl. 39, figs. 1-3 (rev.).

Recognition characters.—Carapace angular, roughly trefoil shaped, from one-third to one-sixth wider than long; surface granulate, uneven. Lateral margin of each side extended into a broad wing projecting over bases of legs; anterolateral margins concave, with notch near middle; posterolateral margins broad, with a deep rounded cavity to each side of intestinal region, extending toward and almost to much smaller pit on dorsal surface at side of cardiac region, a narrow suture connecting cavity and pit of each side. Front narrow, produced, upturned, and with a deep median sinus. Orbits small. A middorsal ridge extending from front almost to posterior margin, ridge interrupted in middle of carapace; branchial region on each side with a prominent elevation more or less divided into two parts, one connected by a ridge to anterior angle of lateral wing, other similarly connected to posterior angle. Hepatic region small, slightly elevated; pterygostomian region prominent, with conical downward-pointing eminence visible from above.

Chelipeds of moderate size, somewhat crested; merus with two large triangular teeth on outer

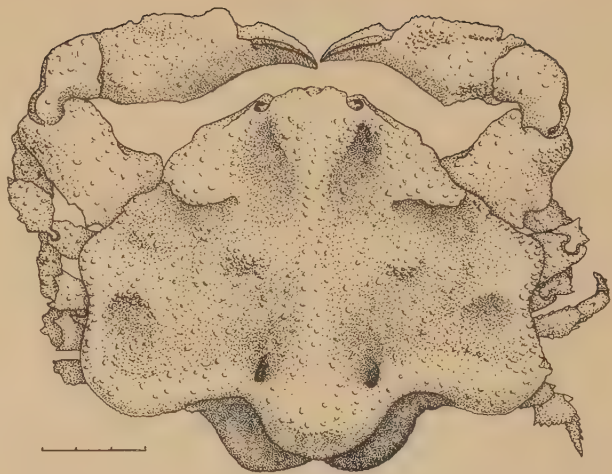


FIGURE 125.—*Speloeophorus pontifer* (Stimpson). Female in dorsal view, 3 mm. indicated.



FIGURE 126.—*Speloeophorus pontifer* (Stimpson). Female in posterior view, 3 mm. indicated.

margin; fingers slender and curved. Walking legs granulate and tuberculate.

Abdomen tuberculate; segments three to five only partially fused; sixth segment with a sharp, backward pointing, proximal spine.

Measurements.—Carapace: length of male, 6 mm., width, 8 mm.; female, length, 10 mm., width, 13 mm.

Variations.—This small species apparently attains a width of about 15 mm., and is extremely variable. The ridges and elevations of the dorsal surface may be sharp and conspicuous or low and rounded; the lateral angles of the lateral wings of the carapace may be produced or rounded off. The female is not so wide in proportion to length as the male, and is somewhat tumid on the outer posterior part of the lateral wings.

Color.—Pale red in middle, remainder white (von Martens in Rathbun, 1937.)

Habitat.—Low tide to 125 fathoms.

Type locality.—Barbados.

Known range.—Off Beaufort, N.C., to west Florida; West Indies to Barbados.

Subfamily *Philyrinae*

Carapace almost hemispherical, surface only slightly uneven. So-called frontal teeth often being well-developed inner-orbital angles. A median frontal tooth often present. Infraorbital lobe seldom well developed, roof of efferent branchial channel usually reaching same level. Epistome usually reduced. Margins of mouth and pterygostomian region in same transverse plane. Merus of external maxillipeds half or more than half length of ischium measured along inner border. First abdominal segment in female often under carapace (Rathbun, 1937).

Genus *Persephona* Leach, 1817

Rathbun, 1937, p. 151.—Hemming, 1958b, p. 18.

Persephona punctata aquilonaris Rathbun. Purse crab

Figure 127

Persephona punctata Stimpson, 1859 (in part), p. 70.—Hay and Shore, 1918 (in part), p. 423, pl. 32, fig. 9.

Persephona punctata aquilonaris Rathbun, 1937, p. 154, pl. 42, figs. 6–7 (rev.).

Recognition characters.—Carapace globular, thickly strewn dorsally and laterally with granules of various sizes, and with three sharp, recurved spines, one at each end of posterior margin and one median just above posterior margin. Front narrow, broadly bidentate, produced and elevated, and with dentiform angles of branchial channels projecting slightly beyond it. Anterior and lateral regions bounded externally by a row of beadlike granules broken anteriorly by a single tubercle of larger size, and posteriorly extending to a point nearly opposite termination of posterior margin.

Chelipeds subcylindrical in adult male, approximately 1.5 times as long as carapace; merus with many large tubercles; carpus and chela nearly smooth except on margins; chela somewhat flat and dilated; fingers weak.

Measurements.—Male: length of carapace to tip of posterior spine, 48 mm.; to base of spine, 45 mm.; width, 42 mm.

Color.—Gray to grayish brown, with darker brownish irregular spots or marmorations; granules white or tinged with red.

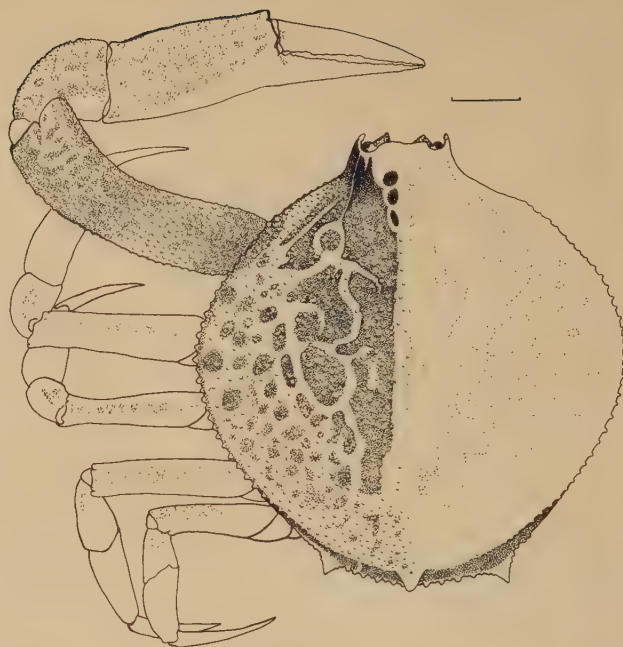


FIGURE 127.—*Persephona punctata aquilonaris* Rathbun. Animal in dorsal view, detail of left side shown, 5 mm. indicated.

Habitat.—This crab is sometimes taken in otter trawls but usually by dredging in shelly mud in relatively shallow water in the ocean; 2 to 30 fathoms.

Type locality.—St. Augustine, Fla.

Known range.—New Jersey to Campeche, Mexico (Hildebrand, 1954, in part).

Remarks.—The species is fairly abundant in colonies. The purselike receptacle formed by the enormously enlarged penultimate segment of the abdomen in the female may be found filled with eggs at almost any time during spring and summer.

Genus *Iliacantha* Stimpson, 1871

Rathbun, 1937, p. 183.

KEY TO SPECIES IN THE CAROLINAS

- a. Fingers longer than palm of hand—*subglobosa* (p. 150).
- aa. Fingers about half as long as palm of hand
intermedia (p. 151).

Iliacantha subglobosa Stimpson

Figure 128

Iliacantha subglobosa Stimpson, 1871a, p. 155.—Hay and Shore, 1918, p. 424, pl. 32, fig. 2.—Rathbun, 1937, p. 185, pl. 53, figs. 1–2 (rev.).

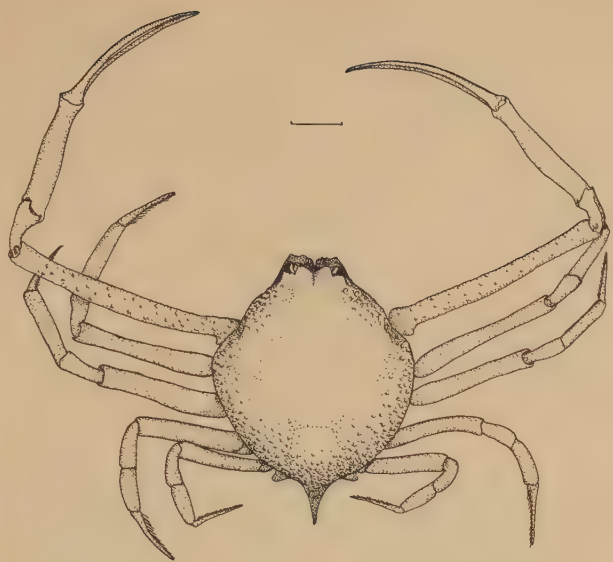


FIGURE 128.—*Iliacantha subglobosa* Stimpson. Female in dorsal view, 5 mm. indicated.

Recognition characters.—Carapace orbicular, smoothly and evenly convex, finely granulate, unarmed except posterior border with three spines; lateral spines subtriangular, blunt; median one higher, longer, conical, and curved upward. Front deeply grooved above, broadly notched anteriorly and with spiniform angles of branchial channels extending beyond it. Margin of carapace distinct, somewhat acute on hepatic region and anterior portion of branchial region, indistinct beyond; hepatic region swollen; intestinal region slightly protuberant above base of median spine.

Chelipeds 2.5 times as long as carapace, excluding spine, finely granulate; merus more sharply granulate than carpus and hand; fingers slender, longer than palm, armed with needlelike teeth. Walking legs slender, smooth; merus as long as three terminal articles; dactyls grooved, and with two fringes of hair on upper and posterior surfaces. Male abdomen gradually tapering from fifth to seventh segment.

Measurements.—Male: carapace length, 21 mm., width, 16 mm.; chela length, 22 mm.; fingers, 13 mm.

Habitat.—Fifteen to 215 fathoms.

Type localities.—Three stations in Florida reefs, 40–80 fathoms.

Known range.—Off Cape Hatteras, N.C., to northwest Florida; through West Indies to Barbados.

Remarks.—Ovigerous females have been taken in June from the Gulf of Mexico.

Iliacantha intermedia Miers

Figure 129

Iliacantha intermedia Miers, 1886, p. 302, pl. 26, figs. 3, 3a.—Hay and Shore, 1918, p. 424, pl. 32, fig. 3.—Rathbun, 1937, p. 186, pl. 54, figs. 1–2 (rev.).

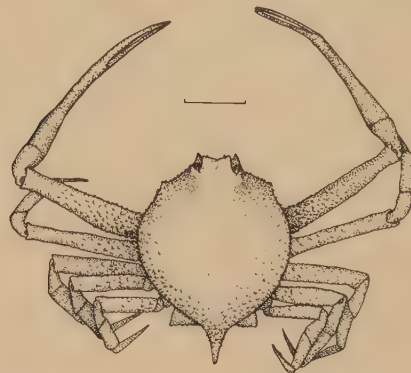


FIGURE 129.—*Iliacantha intermedia* Miers. Male in dorsal view, 5 mm. indicated.

Recognition characters.—Similar to *I. subglobosa*, but carapace more coarsely granulate; posterior spines shorter, flattened, triangular, connected by prominent line of granules. Front deeply grooved above, broadly notched anteriorly, and with spiniform angles of branchial channels extending beyond it. Margin of carapace distinctly granulate; intestinal region not protuberant above median spine.

Chelipeds slender, nearly as long as carapace; merus cylindrical and granulate with coarser granulations proximally; hand smooth, somewhat inflated proximally but tapering to slender fingers; fingers about half as long as palm, incurved at tip, and denticulate on opposed margins. Male abdomen widened at convex-sided sixth segment.

Measurements.—Male: carapace length, 16 mm., width, 12 mm.; chela, length, 13 mm.; fingers, 4 mm. Female: carapace length, 27 mm., width, 21 mm.

Color.—Gray without markings of any kind.

Habitat.—Five and one-half to 180 fathoms.

Type locality.—Bahia, Brazil.

Known range.—Off Beaufort, N.C., to northwest Florida; St. Thomas, V.I.; Venezuela; Bahia, Brazil.

Remarks.—The young of this species and *Persephona punctata aquilonaris* have a close resemblance.

Family Calappidae

Oxystomata of normal crablike form with abdomen hidden beneath thorax. Antennae small. Afferent openings of gill chambers in front of chelipeds. Outer maxillipeds not completely closing buccal cavity. Male openings coxal on fifth pair of legs.

Calappid species are known from the Cretaceous to the present in North America (Rathbun, 1935).

KEY TO GENERA AND ONE SPECIES IN THE CAROLINAS

- a. Posterolateral region of carapace expanded and dentate
Calappa (p. 152).
- aa. Posterolateral region of carapace not expanded.
 - b. Merus bispinous on distal outer surface with lower spine strong and greatly extended laterally
Acanthocarpus alexandri (p. 156).
 - bb. Merus not bispinous or distal outer surface.
 - c. Carapace considerably broader than long, regularly convex above.....*Hepatus* (p. 157).
 - cc. Carapace nearly as long as broad, dorsal surface uneven.....*Osachila* (p. 159).

Subfamily Calappinae

Merus of external maxillipeds almost never elongate and acute, never concealing palp in repose. Legs adapted for walking (Alcock in Rathbun, 1937).

Genus *Calappa* Weber, 1795

Rathbun, 1937, p. 197.

KEY TO SPECIES IN THE CAROLINAS

- a. Carapace widest behind middle; proximal tooth on lower edge of hand with margin pointed or angled.
- b. Carapace smoothly granulate.
 - c. Carapace often with a horizontal tooth or spine at either end of posterior margin; smooth area on lower half of palm on cheliped narrow proximally, widening and continued obliquely upward distally
sulcata (p. 155).
 - cc. Carapace without a horizontal tooth or spine at either end of posterior margin; smooth area on lower half of palm on cheliped concave, not directed obliquely upward distally.
- d. Male with basal width of fifth abdominal segment twice median length; female with a few granulations near lateral border of fourth abdominal segment.....*flammea* (p. 152).

dd. Male with basal width of fifth abdominal segment less than twice median length; female with no granulations near lateral border of fourth abdominal segment.....*ocellata* (p. 153).

bb. Carapace covered with rough protuberances, and granulate.....*angusta* (p. 154).

aa. Carapace widest in front of middle; proximal tooth on lower edge of hand with margin not pointed or angled.....*angusta* (young) (p. 154).

Calappa flammea (Herbst)

Figures 130-131

Cancer flammeus Herbst, 1794, p. 161, pl. 40, fig. 2.

Calappa flammea: Hay and Shore, 1918, p. 421, pl. 31, fig. 8.—Holthuis, 1958, p. 148, figs. 28-35 (rev.).



FIGURE 130.—*Calappa flammea* (Herbst). Female from Tortugas, Florida, in dorsal view, approximately $\times 0.66$ (after Holthuis, 1958).

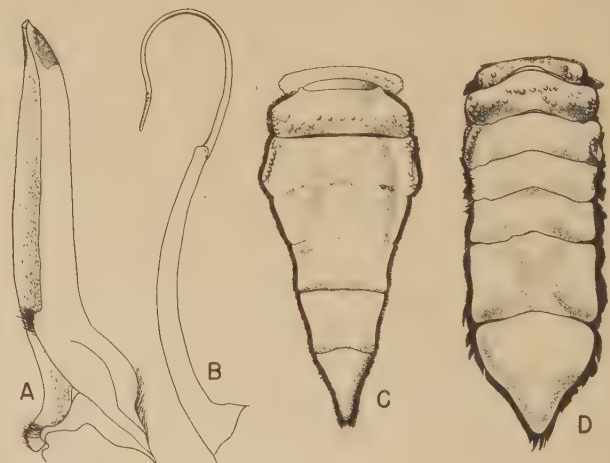


FIGURE 131.—*Calappa flammea* (Herbst). A, male first pleopod in ventral view, $\times 3$; B, male second pleopod in dorsal (anterior) view, $\times 3$; C, abdomen of male, approximately $\times 0.8$; D, abdomen of female, approximately $\times 0.8$; A-C from Tortugas, D from Bahama Islands (after Holthuis, 1958).

Recognition characters.—Carapace 1.14 to 1.42 times broader than long, varying from smaller to larger ratio with increasing size; surface granular, less conspicuously so in posterior half, tuberculate anteriorly, becoming obsolescent in adults; branchiocardiac grooves distinct. Front deeply notched anteriorly, projecting somewhat beyond orbits; anterolateral borders together forming a semicircle in younger specimens, less strongly arched in adults. Posterolateral winglike expansions of carapace distinct, consisting of five broad teeth with beaded edges, second and third with sharp but not pointed apices, fifth tooth with notch on inner basal part.

Chelipeds with outer surface of palm divided into three horizontal zones: a lower one with many large granules; a second zone, slightly sunken, with no large granules but with scattered small ones, more in males than females; a third zone occupying whole upper half of outer surface of palm, separated from second zone by a row of small granules, bearing many small granules, and some large low granular tubercles, more densely granulated than second zone in females, same in both in males. Upper margin of large hand with about seven teeth, six on small hand; proximal teeth broad, low, and bifurcated. Palm with strong tooth on outer lower surface near carpus, apex of tooth approximately rectangular with a sharp tip. Fingers of crushing hand somewhat stouter than on cutting hand, and with prominent projecting lobule near base of each. Merus with strong four-toothed crest parallel with outer distal border.

Male with abdomen narrow; third to fifth segments fused, fifth segment with basal width twice median length, sixth with width greater than length, seventh with length about 1.5 times width. Female with a few granulations near lateral border of fourth segment; length of seventh segment equal to or slightly greater than width.

Measurements.—Carapace: male, length, 99 mm., width, 136 mm.; female, length, 106 mm., width, 135 mm.

Color.—Ground color of carapace gray behind, shading to drab mottled with white over greater portion; reddish blue on outer surface of chelipeds becoming almost white on lower half of palm and on fingers; inner surface of chelipeds, pterygostomian regions, anterior surface of first walk-

ing legs, and a small part of second walking legs reddish hued. Carapace with color pattern variable, purplish brown in interlacing bands on anterior half, obliquely longitudinal stripes on posterior half becoming lighter posteriorly. Merus, carpus, and proximal upper portion of palm striped with purplish brown, two distinct round spots of same color in middle of palm; upper half of palm with spots and patches of sulphur yellow on teeth and tubercles and same color mixed with ground color of merus, carpus, and part of carapace; two or three orange spots on hands near base of dactyls and spots of same near articulation of palm and carpus. Third to fifth legs, and underparts whitish. (Adapted from R. L. Barney in Rathbun, 1937.)

Habitat.—This strikingly colored crab does not often occur within the harbor at Beaufort, N.C., but is often brought up from a few fathoms outside the inlet. Those obtained inside are usually small. Hildebrand (1955) listed the species as common from 6 to 16 fathoms on the Campeche Banks. The species may spend much time buried in sand (Pearse, Humm, and Wharton, 1942).

Habitat.—Surface to 40 fathoms, rarely to 125 fathoms.

Type locality.—America.

Known range.—Cape Hatteras, N.C., to Florida Keys; Gulf coast of United States and Mexico; Bahamas; Bermuda.

Remarks.—This species has a fossil record in North America dating from the Oligocene (Rathbun, 1930b).

The breeding range of the species extends as far northward as Cape Hatteras, but in the larval stages it often drifts as far to the north as southern New England. Some of these larvae are supposed now and then to survive a mild winter and develop by the next summer into the small specimens which have at rare intervals been taken on the coast of Massachusetts and Rhode Island. Some of the larval stages have been figured by Lebour (1944). Smith (1880b) gave a description of the megalops stage of this species.

Calappa ocellata Holthuis

Figures 132-133

Holthuis, 1958, p. 158, figs. 36-40 (rev.).

Recognition characters.—Carapace slightly narrower than in *C. flammea*, having width to



FIGURE 132.—*Calappa ocellata* Holthuis. Male from Curaçao in dorsal view, approximately natural size (after Holthuis, 1958).

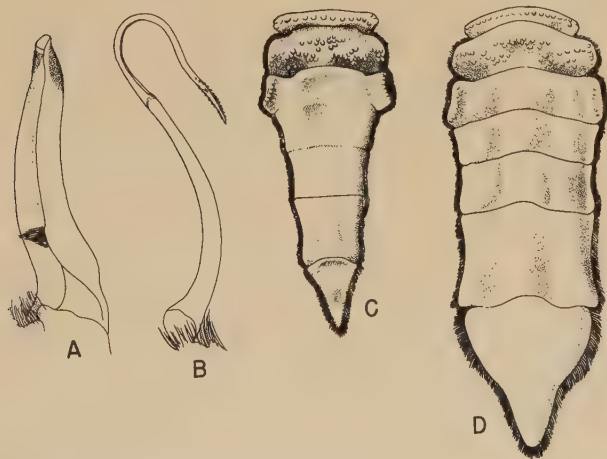


FIGURE 133.—*Calappa ocellata* Holthuis. A, male first pleopod in ventral view, $\times 3$; B, male second pleopod in dorsal (anterior) view, $\times 3$; C, abdomen of male, approximately $\times 0.8$; D, abdomen of female, approximately $\times 0.8$; A-D from Dutch West Indies (after Holthuis, 1958).

length ratio of 1.15 to 1.40, varying from smaller to larger ratio with increasing size; granulations much coarser than in *C. flammea*, granules larger, fewer, and more widely separated. Posterolateral winglike projections distinctly set off from anterolateral margin, teeth with slender pointed tips, more slender than in *C. flammea*, notch in basal part of fifth tooth inconspicuous.

Chelipeds similar to *C. flammea*, though second and third zones of outer palm nearly alike in both

males and females. Upper margin with teeth narrower proximally than in *C. flammea*, and with bifurcation indistinct or absent. Palm with strong tooth on outer lower surface near carpus, apex sharply pointed with an acute tip. Teeth on crest of merus more sharply pointed than in *C. flammea*.

Male with abdomen narrower than in *C. flammea*; third to fifth segments fused, fifth segment with basal width less than twice median length, sixth with width equal to or less than length, seventh more slender than in *C. flammea*. Females with no granules near lateral border of fourth segment; length of seventh segment distinctly greater than width.

Measurements.—Male holotype: length of carapace, 83 mm.; width, 114 mm.

Color.—In preserved specimens, anterior half of carapace red with numerous white, often ocellated, spots and a few white streaks, the whole forming a reticulate pattern of red. Pattern more compact and complete than in *C. flammea*, extending over full width of anterior half of carapace, absent in posterior half showing only a few distinct spots between teeth of posterolateral wings, and two red spots before posterior margin above bases of last legs. Chelipeds with one or two red spots near articulation of dactyls; red between teeth of upper margin; inside of chelipeds reddish (Holthuis, 1958).

Habitat.—Shallow water to 14 fathoms.

Type locality.—Klein Bonaire, Dutch West Indies.

Known range.—Cape Hatteras, N.C., to State of Pernambuco, Brazil; Bermuda.

Remarks.—This species is less common than *C. flammea* from Tortugas northward (Holthuis, 1958).

Calappa angusta Milne Edwards

Figure 134

Calappa angusta Milne Edwards, 1880, p. 18.—Hay and Shore, 1918, p. 421, pl. 31, fig. 7.—Rathbun, 1937, p. 210, pl. 64, figs. 1-6 (rev.).

Recognition characters.—Carapace eight-ninths as long as wide; anterolateral margins finely granulate with larger granules at intervals; surface covered with protuberances, granulate between. Tooth at posterolateral angle of winglike extension of carapace largest, preceded anteriorly by four teeth gradually diminishing in size, and followed posteriorly by one small and one or two



FIGURE 134.—*Calappa angusta* Milne Edwards. Animal from North Carolina in dorsal view, approximately $\times 1.8$.

extremely small teeth. Orbit completely separated from antennular cavity.

Chelipeds with outer surface of palm divided into three zones as in preceding species; upper margin with six to eight teeth. Abdomen with sixth segment subquadrate; seventh segment subtriangular, slightly longer than wide.

Measurements.—Carapace: male, length, 28 mm., width, 32 mm.; female, length, 23 mm., width, 28 mm.

Variations.—Posterior part narrower than middle of carapace in juveniles, wider than middle in adults.

Color.—Ground color buff to buff yellow; high spots or lumps on carapace and chelipeds red. Marginal spines of carapace, crest of chela and lumps on crest drab. Hairs of carapace, especially those of hind margin, light olive yellow; those of walking legs light citrous yellow. Merus of chelipeds practically colorless. Under parts whitish, pterygostomial region and maxillipeds suffused with pale purple (Schmitt in Rathbun, 1937).

Habitat.—More abundant in the Gulf Stream than in adjacent inshore waters; 7.5 to 115 fathoms, rarely deeper.

Type locality.—Barbados.

Known range.—Off Cape Lookout, N.C., through eastern Gulf of Mexico, to Grenada.

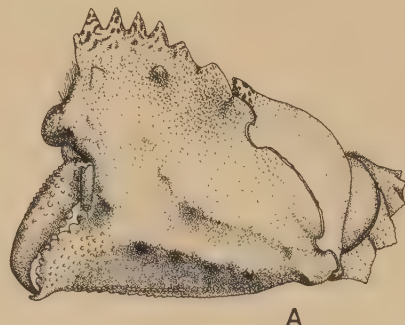
Remarks.—Ovigerous females have been taken from southern Florida in March.

Calappa sulcata Rathbun

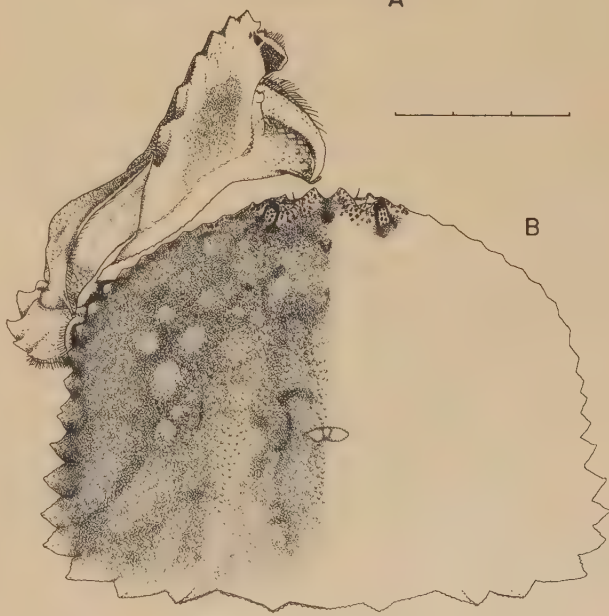
Figures 135–136

Calappa sulcata Rathbun, 1898, p. 289, pl. 9, figs. 3–4.—Hay and Shore, 1918, p. 422, pl. 31, fig. 6.—Holthuis, 1958, p. 179, figs. 51–54 (rev.).

Recognition characters.—Carapace somewhat wider than long, covered with uniform granulations giving appearance of being smooth. Anterolateral margins crenulate and granulate, grading into inconspicuous anterolateral wings; teeth triangular, pointed. Posterior margin with tooth at each end near base of abdomen, sharper in males than in females, very low in adults, most slender and sharp in juveniles; third tooth of posterolateral wings extremely sharp and slender, pointed in juveniles.



A



B

FIGURE 135.—*Calappa sulcata* Rathbun. A, large chela in external view; B, female in dorsal view; 30 mm. indicated.

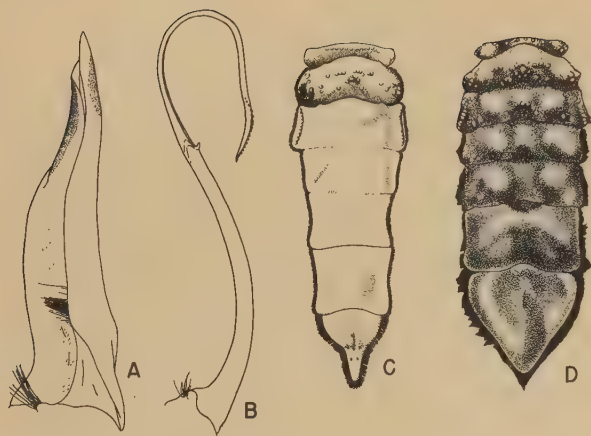


FIGURE 136.—*Calappa sulcata* Rathbun. A, male first pleopod in ventral view, approximately $\times 3$; B, male second pleopod in dorsal (anterior) view, approximately $\times 3$; C, abdomen of male, approximately $\times 0.8$; D, abdomen of female, approximately $\times 0.6$; A–C from near Margarita Island, Venezuela; D from Surinam (after Holthuis, 1958).

Chelipeds with outer surface of palm divided into three zones as in preceding species; large tubercles of lower zone low and inconspicuous; zones one, two, and three each separated by a row of sharply pointed tubercles; middle zone not extending horizontally, but curving dorsally in distal part, smooth, with minute granules; zone three smooth, except for two low, inconspicuous, granular tubercles near upper margin of palm; granulations on palm more distinct in females than in males; tooth on outer, lower, proximal surface of palm nearly rectangular in large individuals, slender and acute in smaller ones. Meral articles of walking legs with granules on lower surface.

Measurements.—Carapace: male, length, 77 mm., width, 98 mm.; female, length, 92 mm., width, 119 mm.

Color.—In alcohol, often light pinkish brown with small, narrow rings of dark red, median ring most conspicuous; each carpus with a ring, and each palm with one near upper margin enclosing tubercle toward proximal end of margin (Rathbun, 1937).

Habitat.—Twelve to 100 fathoms (Ceramé-Vivas, personal communication).

Type locality.—Off Louisiana, lat. $29^{\circ}24'30''$ N., long. $88^{\circ}01'$ W., depth, 35 fathoms.

Known range.—Cape Hatteras, N.C., to Gulf of Mexico; through West Indies to French Guiana.

Remarks.—Hildebrand (1954) reported this species (under the name *C. springeri*) as conspicuous but never abundant in the western and northwestern Gulf of Mexico at depths of 12 to 35 fathoms. One ovigerous female was found in May off Padre Island, Tex.

Genus *Acanthocarpus* Stimpson, 1871

Rathbun, 1937, p. 220.

Acanthocarpus alexandri Stimpson

Figure 137

Acanthocarpus alexandri Stimpson, 1871a, p. 153.—Rathbun, 1937, p. 221, pl. 69, figs. 1–2 (rev.).

Recognition characters.—Carapace ovate, regularly convex, widest in anterior half; surface uneven, granulate, and punctate, with protuberances arranged longitudinally in roughly five rows centrally, and two shorter, intercalated rows behind orbits; all rows formed into ridges, those adjacent to midline each terminating in a spine on postero-lateral margin. Posterior margin arcuate bearing a low eminence at middle; inferior margin of pterygostomian region with a row of 7 to 11 strong, widely spaced, oblique ridges of varying length. Orbits large, margins ciliated.

Chelipeds strong; merus bispinose on distal outer surface, inferior spine strong and a little longer or shorter than half width of carapace, superior spine one-fourth to one-third length of inferior spine; hand with superior crest of 7 closely placed teeth, and an oblique 6-toothed crest on outer surface extending from base of dactyl to postero-inferior angle, scattered tubercles between crests; inner surface of hand with stridulating ridge composed of about 45 oblique, closely placed striae which can be played against oblique ridges of pterygostomian region. Walking legs smooth. Sternal plastron with a conical tubercle on either side of first article.

Measurements.—Male carapace: length, 13 mm.; width, 32 mm.

Color.—Dorsal surface of carapace and chelipeds pale reddish orange, deepest in hue on elevations of carapace and bases of meral spines of chelipeds; underparts white, slightly tinged with red (Rathbun, 1937).

Habitat.—Thirty-seven to 208 fathoms.



FIGURE 137.—*Acanthocarpus alexandri* Stimpson. Male in dorsal view, walking legs of left side not shown, 10 mm. indicated.

Type locality.—Off the Quicksands, Florida Keys, 74 fathoms.

Known range.—Georges Bank off Massachusetts to west coast of Florida; Puerto Rico to Grenadines; Brazil (Da Costa, 1959).

Remarks.—The species has been recorded off both Carolinas, usually at depths greater than 100 fathoms. One collection was taken off South Carolina in 1950 at 60–65 fathoms along with *Sicyonia* and *Hymenopenaeus* sp.

Rathbun (1937) reported ovigerous females in June and July from Florida.

Subfamily Matutinae

Merus of external maxillipeds elongate and acute, entirely concealing palp in repose (Alcock in Rathbun, 1937).

Genus *Hepatus* Latreille, 1802

Rathbun, 1937, p. 234.—Holthuis, 1959, p. 173.

KEY TO SPECIES IN THE CAROLINAS

- a. Carapace covered with small spots; front bidentate
pudibundus (p. 157).
- aa. Carapace covered with large spots; front truncate
epheleticus (p. 158).

Hepatus pudibundus (Herbst)

Figures 138–139

Cancer pudibundus Herbst, 1785, p. 199.

Hepatus princeps: Rathbun, 1937, p. 235, pl. 70, figs. 1–2 (rev.).

Hepatus pudibundus: Holthuis, 1959, p. 167, figs. 36–38a, b (rev.).

Recognition characters.—Carapace between two-thirds and three-fourths as long as broad, relatively narrower in juveniles than in adults,

covered with transverse lines or small spots, strongly convex. Surface smooth in adults; juveniles with eight distinct rows of tubercles, three in a transverse line in broadest part of carapace, two others in front and three behind. Front thick, obtuse, slightly bidentate. Anterolateral margin divided into 12 or 13 more or less rectangular teeth, denticulate on margins and not projecting; anterior portion of posterolateral margin consisting of 2 rows of tubercles placed side by side with no space between, a small tooth in middle of rows and another in posterior portion of this margin.

Outer face of hands with five rows of tubercles exclusive of marginal ones. Dactyls of walking legs with a coating of short, dense pubescence, except for tip, and a narrow smooth line on each side.

Measurements.—Carapace: males, length, 16–55 mm., width, 21–76 mm.; females, length, 14–46 mm., width, 18–62 mm. (Holthuis, 1959).

Color.—"Pale yellowish brown, with dark-brown transverse lines, or transverse series of spots; legs subochreous [sic], with one or two large purplish blotches in each joint." (Dana in Rathbun, 1937.) Holthuis (1959) gave the color in preserved specimens. Carapace covered with small reddish dots, scattered or sometimes arranged into transverse bands or lines, larger posteriorly than anteriorly; similar dots on carpus and palm; walking legs with two conspicuous broad bands of reddish color on merus, one on carpus and one on propodus, meral bands most distinct on last leg.



FIGURE 138.—*Hepatus pudibundus* (Herbst). Female in dorsal view, approximately natural size (after Holthuis, 1959).

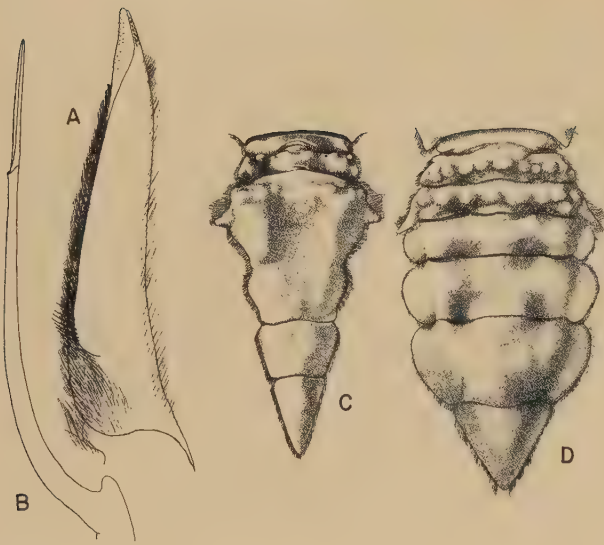


FIGURE 139.—*Hepatus pudibundus* (Herbst). A, male first pleopod; B, male second pleopod; A-B approximately $\times 8$; C, abdomen of male; D, abdomen of female; C-D approximately $\times 2$ (after Holthuis, 1959).

Habitat.—Beach to 6 fathoms.

Type locality.—Martinique.

Known range.—Georgia to State of São Paulo, Brazil.

Remarks.—Holthuis (1959) reported an ovigerous female in April from Surinam. Several of the specimens Holthuis studied carried one or more sea anemones on the carapace and one bore barnacles.

Hepatus epheliticus (Linnaeus) Calico crab, Dolly Varden crab

Figure 140

Cancer epheliticus Linnaeus. 1763, p. 414.

Hepatus epheliticus: Hay and Shore, 1918, p. 422, pl. 37, fig. 1.—Rathbun, 1937, p. 238, pl. 70, figs. 3-4; pl. 71, figs. 1-4 (rev.).

Recognition characters.—Carapace covered with large spots, about two-thirds as long as wide, convex above, regularly arcuate in front, strongly narrowed behind, almost smooth, with indistinct lines of low granules on gastric region and posterior part of branchial region. Front narrow, truncate, tuberculate, not dentate, and placed higher than continuation of anterolateral borders of carapace; anterolateral borders dentate with denticles more prominent than in *H. pudibundus*, middle denticle of each tooth projecting.

Chelipeds moderately strong; carpus and hand with lines of coarse tubercles on outer face and a

three- to four-toothed crest on superior margin of hand. Dactyls of walking legs with a coating of short, dense pubescence except for tip and a narrow smooth line on each side.

Measurements.—Carapace of male: length, 46 mm.; width, 67 mm.

Variations.—In a series representing various ages a great deal of variation is shown, the granulations being relatively much coarser and the spots more numerous and variable in color in juveniles.

Color.—Dark gray or brownish with numerous, rather large, round or irregular spots of light red (muddy lavender to light red in young) with darker borders scattered over carapace.

Habitat.—This species is often found in depths of a few fathoms in channels of Beaufort, N.C., harbor, though such individuals are not so numerous or large as those taken in the ocean outside. Gunter (1950) found the species in water ranging from 28.7 to 35.2‰. Two to 25 fathoms.

Type locality.—Carolina.

Known range.—Chesapeake Bay to Gulf of Campeche, Mexico; Cuba; Jamaica; Dominican Republic.

Remarks.—Though recorded in depths to 25 fathoms, Hildebrand (1954, 1955) found this species most common shoreward of 12 fathoms in



FIGURE 140.—*Hepatus epheliticus* (Linnaeus). Male in dorsal view, legs of left side not shown, 20 mm. indicated.

Texas and Mexico. He found ovigerous females rare, but occurring in July, and noted a common occurrence of the sea anemone, *Calliactis tricolor*, on the carapace, as found also by Carlgren and Hedgpeth (1952).

Gray (1957) found that *H. epheliticus* has a large gill area in relation to its weight. He related this large respiratory area to its active nature as compared to other strictly aquatic crabs.

Costlow and Bookhout (1962b) described five zoeal and one megalops stage from individuals hatched and reared at 25° C. in an array of salinities ranging from 20 to 40 ‰. Complete development took place only at 30 and 35 ‰ though some growth occurred in the other salinities. The authors pointed out that the adults are usually found in waters with salinity in the 30–35 ‰ range.

Genus *Osachila* Stimpson 1871

Rathbun, 1937, p. 248.—Hemming, 1958b, p. 17.

KEY TO SPECIES IN THE CAROLINAS

- a. Posterolateral margin of carapace thin edged, almost sharp-----*tuberosa* (p. 159).
- aa. Posterolateral margin of carapace thick, blunt
semilevis (p. 159).

Osachila tuberosa Stimpson

Figure 141

Osachila tuberosa Stimpson, 1871a, p. 154.—Hay and Shore, 1918, p. 423, pl. 31, fig. 10.—Rathbun, 1937, p. 250, pl. 77, fig. 3 (rev.).



FIGURE 141.—*Osachila tuberosa* Stimpson. Male in dorsal view, 3 mm. indicated.

Recognition characters.—Carapace octagonal, with six large protuberances, one mesogastric, paired metagastric, one cardiac, paired mesobranchial; protuberances and lateral margins finely eroded. Anterolateral margins finely dentate, continued toward buccal cavity; posterolateral margins thin edged, with four lobes, first lobe projecting sideways slightly beyond adjacent anterolateral tooth. Front usually with a narrow sinus. Maxillipeds, sternum, abdomen, and bases of legs eroded.

Chelipeds short, thick, tuberculate on outer face, and with rough margins; hand stout, upper margin with three teeth, proximal one bifid; immovable finger thick. Walking legs more or less prismatic with sharp margins and light longitudinal grooves.

Measurements.—Carapace of female: length, 18 mm.; width, 20 mm.

Color.—"Sand color with reddish cast, white below, claws and legs white." (Henderson in Rathbun, 1937.)

Habitat.—Forty to 65 fathoms.

Type locality.—Five stations among the Florida reefs, 36–68 fathoms.

Known range.—Off Cape Hatteras, N.C., to west Florida.

Remarks.—This southern species has been recorded only once from North Carolina.

Osachila semilevis Rathbun

Figure 142

Osachila semilevis Rathbun, 1916, p. 652, pl. 36, fig. 1.—Hay and Shore, 1918, p. 422, pl. 31, fig. 9.—Rathbun, 1937, p. 251, pl. 77, fig. 1 (rev.).

Recognition characters.—Much like *O. tuberosa*. Carapace octagonal, with six large protuberances, one mesogastric, paired metagastric, one cardiac, paired mesobranchial; protuberances eroded, depressions nearly smooth. Anterolateral margins finely dentate, continued toward buccal cavity; posterolateral margins thick, with four lobes; first lobe not projecting laterally so far as adjacent anterolateral lobe; last lobe quite prominent. Front usually with a narrow buttonholelike sinus.

Chelipeds short, thick, tuberculate on outer face and with rough margins; hand stout, upper margin with three simple teeth; immovable finger thick, dactyl comparatively slender and straight. Walking legs of moderate size, more or less

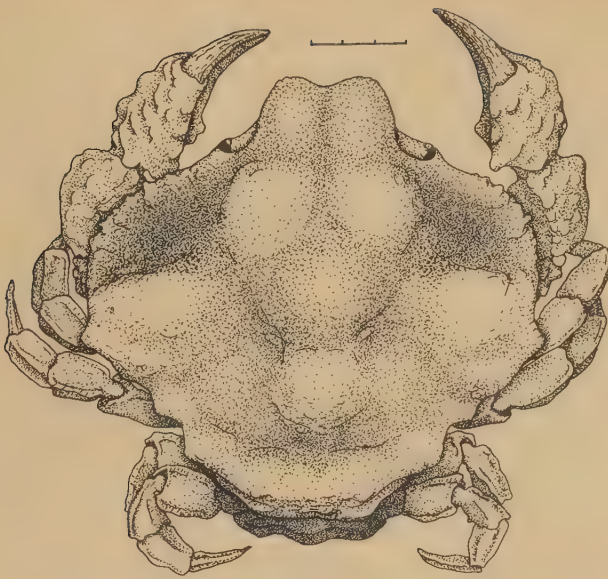


FIGURE 142.—*Osachila semilevis* Rathbun. Animal in dorsal view, 3 mm. indicated.

prismatic and lightly grooved. Abdomen narrow, eroded along margins and on last two segments.

Measurements.—Carapace of ovigerous female: length, 13 mm.; width, 15 mm.

Habitat.—Thirteen to 50 fathoms.

Type locality.—Gulf of Mexico, 25 fathoms.

Known range.—Off Beaufort, N.C., to northwest Florida.

Remarks.—This southern species has been recorded north of Florida only twice, both times from the Beaufort, N.C., area. Ovigerous females have been taken from Florida in July.

Subsection **Brachygnatha**

Brachyura having buccal frame roughly quadrate. Last pair of legs normal in form, rarely reduced in size, and almost never dorsal. Gills few. First abdominal appendages of female absent, female openings sternal.

Superfamily **Brachyrhyncha**

Fore part of body broad, rostrum reduced or absent; body oval, round, or square, usually broader than long. Orbits nearly always well enclosed.

Family **Portunidae**. The swimming crabs

Crabs with body transversely oval, usually five to nine lateral teeth. Last pair of legs usually dis-

tinctly adapted for swimming, with terminal article ovate, flattened.

The family has a fossil record in America dating from the Cretaceous (Rathbun, 1935).

Stephenson and Campbell (1960) discussed the status of portunid subfamily names in the light of recent action by the International Commission on Zoological Nomenclature. This decision altered the usage of Rathbun (1930a) in that the subfamilies Liocarcininae and Thalamitinae become respectively Macropipinae and Portuninae.

KEY TO GENERA AND SOME SPECIES IN THE CAROLINAS

- a. Carapace with five teeth of about equal size on anterolateral margin; interocular teeth three (Subfamily Macropipinae)-----*Ovalipes* (p. 160).
- aa. Carapace with nine anterolateral teeth, lateral tooth usually much larger than others; interocular teeth four, six, or eight (Subfamily Portuninae).
- b. Movable portion of antenna not excluded from orbit.
- c. Palate with longitudinal ridge.
- d. Abdomen of male more or less triangular
Portunus (p. 162).
- dd. Abdomen of male with last two segments much narrower than basal segments
Callinectes (p. 168).
- cc. Palate without longitudinal ridge
Arenaeus cribrarius (p. 173).
- bb. Movable portion of antenna excluded from orbit by prolongation of basal article; anterolateral teeth alternately large and small---*Cronius ruber* (p. 174).

Subfamily **Macropipinae**

Genus ***Ovalipes*** Rathbun, 1898

Rathbun, 1930a, p. 18.

KEY TO SPECIES IN THE CAROLINAS

- a. Carapace yellowish gray, closely set with small annular spots of reddish purple; iridescent spots between each pair of anterolateral spines approximately alike in size and shape-----*ocellatus* (p. 160.)
- aa. Carapace yellowish gray, without ocellated spots; iridescent spot between fourth and fifth anterolateral spines large and nearly semicircular in shape
guadalupeensis (p. 161).

Ovalipes ocellatus (Herbst)

Figure 143

Cancer ocellatus Herbst, 1799, p. 61, pl. 49, fig. 1.
Ovalipes ocellatus ocellatus: Hay and Shore, 1918, p. 426, pl. 32, fig. 7.—Rathbun, 1930a, p. 19, pls. 2-3 (rev.).
Ovalipes ocellatus: Williams, 1962, pp. 39-41.

Recognition characters.—Carapace about one-fourth wider than long, convex, finely granulate



FIGURE 143.—*Ovalipes ocellatus* (Herbst). Male in dorsal view, approximately $\times 0.80$ (after Rathbun, 1884).

overall except for longitudinal band of slightly enlarged granules in median line and smooth area on posterior central portion of adults. Front with three acute teeth, median one about twice as long as lateral ones. Orbit with a shallow fissure above, often nearly closed in adults, open in young. Five anterolateral teeth strong, acute, directed forward; inner suborbital angle projecting at least as far as median frontal tooth. Pterygostomian region with a long, curved, stridulating ridge made up of approximately 50 close-set striae narrowing into tubercles at inner end of ridge, a short complementary ridge on proximal end of inner margin of merus; lobe at distal inner angle of merus of outer maxilliped longer than broad.

Chelipeds rather large; distal three-fifths of anterior margin of merus with several small spines and a dense fringe of hair; carpus with two spines, inner one very long; hand triangular in section, external border costate, covered with uniform small tubercles, internal border with an overhanging densely hairy ridge ending distally in a sharp spine, ridges and internal line of hairs continued on dactyl; fingers about as long as palm, tapering gradually, tips turned abruptly toward each other.

Abdomen of male narrow, sides nearly parallel; sixth segment nearly twice as long as seventh in midline, seventh segment subcircular; first pleopods of male broad and stout in proximal two-thirds, narrowing abruptly distally and with terminal portion bent ventrolaterally in a sinuous curve. Abdomen of adult female suboval and small compared to sternum.

Measurements.—Carapace: males, length, 64 mm., width, 77 mm.; female, length, 39 mm., width, 48 mm.

Variations.—Spines are more acute on young than on old individuals, and on some old adults the anterolateral spines are worn away leaving only rounded humps. The orbital fissure is nearly closed in adults but often open in young individuals. The width between the suborbital angles tends to increase relatively with age.

Color.—"Yellowish gray, closely set with small annular spots of reddish purple; carapace and chelipeds with a silvery or brassy iridescence; ground color of chelipeds and legs light brownish tending to orange and bluish; large irregular bluish purple spots on upper surface of chelipeds; large part of carpus including spine bluish; similar but lighter spots on proximal half of other legs; paddles greenish yellow, with deep yellow rim" (Rathbun, 1930a, and other authors). An iridescent spot between each pair of anterolateral spines.

Habitat.—Common on a variety of bottoms, especially sand; surface to 18 fathoms.

Type locality.—Long Island near New York.

Known range.—Prince Edward Island, Canada (E. L. Bousfield, personal communication), to Charleston, S.C., and on Texas coast jetties (Whitten, Rosene, and Hedgpeth, 1950).

Remarks.—The distinctions between this species and *O. quadulpensis* were discussed by Williams (1962). There is a distinct color difference, pointed out in the color descriptions, and an apparent difference in habitat among the adults. Adults of *O. ocellatus* are found near shore in the Carolinas where the young of both species are also found, as pointed out by a number of authors.

Pearse, Humm, and Wharton (1942) pointed out that *O. ocellatus* can bury itself completely in sand and respire by passing water into the gill cavity from anterior lateral openings, then out through two posterior openings. Gray (1957) correlated great activity of the species with large gill area and compared this with gill areas of other strictly aquatic crabs.

Ovalipes quadulpensis (Saussure)

Portunus quadulpensis Saussure, 1858, p. 433, pl. 2, fig. 10.

Ovalipes ocellatus floridanus Hay and Shore, 1918, p. 427, pl. 32, fig. 8.

Ovalipes ocellatus quadulpensis: Rathbun, 1930a, p. 23, pl. 4 (rev.).

Ovalipes quadulpensis: Williams, 1962, pp. 39–41.

Recognition characters.—Closely resembling *O. ocellatus*, but differing in the following characters: dorsal aspect of carapace not covered with ocellated spots; body flatter than *O. ocellatus*, and carapace evenly granulate overall except for smooth area on rear central portion; outer orbital and frontal teeth more acute than in *O. ocellatus*, median frontal tooth acuminate; iridescent spot between fourth and fifth anterolateral spines larger than spots between first to fourth teeth and nearly semicircular in shape; external ridge on palm of chelipeds with tubercles not uniform in size giving a roughened appearance in individuals larger than 30 mm. in width.

Measurements.—Carapace: male, length, 67 mm., width, 82 mm.; female, length, 56 mm., width, 67 mm.

Variations.—The distance between the sub-orbital angles tends to increase relatively with age.

Color.—"General color of carapace light lavender gray underlaid with dull yellow, some specimens darker or lighter, with a regular pattern of lighter spots dull yellow, off white, or bluish yellow to lavender yellow, rear border of carapace light blue; spines of carapace purplish red at base to red or purple subdistally, white at tips; carpus and merus of chelipeds somewhat same color as carapace except pink flesh colored at carpo-meral joint and on hand; fingers white on inner surface, and with white teeth; large spine at internal angle of carpus and a few small but distinct spots on superoexternal surface of hand purple, large spine grading to lighter purple on body of carpus; anterior border of chela and first three pairs of walking legs with a longitudinal band of brownish purple, band extending to lower border of dactyl on chela; dactyls of first three walking legs and outer border of hand immediately below external ridge, same color, sometimes darker on dactyl with teeth same color, distal tip of immovable finger similarly colored; blade of swimming leg yellowish; underparts light.

"Iridescent spots between anterolateral teeth, on distal or dorsal surface of external carpal spine and along upper edge of hand, at superodistal corner of merus on first three walking legs and along dorsal edge of first three pairs of walking legs distally, or dorsal surface of second abdom-

inal segment; spot between fourth and fifth anterolateral spines nearly semicircular" (Williams, 1962).

Habitat.—Taken on sandy bottom in the Carolinas and from similar bottoms elsewhere, according to literature records; surface to 49 fathoms (rarely to 925 fathoms?).

Type locality.—Guadeloupe.

Known range.—Cape Hatteras, N.C., to Port Aransas, Tex.; Guadeloupe; Brazil.

Remarks.—The distinctions between this species and *O. ocellatus* were discussed by Williams (1962). There is a distinct color difference, pointed out in the color descriptions, and an apparent difference in habitat among the adults. Adults of *O. guadulpeensis* are found farther from shore than adults of *O. ocellatus* in the Carolinas, but the young of both species are found near shore, as pointed out by a number of authors.

Ovigerous females are known from North Carolina in January.

Subfamily Portuninae

Genus *Portunus* Weber, 1795

Rathbun, 1930a, p. 33.—Hemming, 1958b, p. 133.—Stephenson and Campbell, 1959, p. 85.

Stephenson and Campbell (1959) gave a number of arguments for and against the utility of subgeneric limitations within this genus as now understood. Though subgeneric subdivisions may be useful in the limited Carolinian fauna, they are being deleted here.

KEY TO SPECIES IN THE CAROLINAS

- a. Carapace wide; anterolateral margins forming arc of a circle with center near posterior margin of carapace.
- b. Interocular teeth six, inner orbital tooth being entire.
- c. Carapace convex, mostly smooth and glossy; palms swollen, only one spine on upper margin in addition to spine at base of dactyl.....*sayi* (p. 163).
- cc. Carapace uneven, not smooth and glossy; two spines on upper margin of palm in addition to spine at base of dactyl.....*anceps* (p. 163).
- bb. Interocular teeth eight, inner orbital tooth being bilobed.....*gibbesii* (p. 164).
- aa. Carapace narrow; anterolateral margins forming arc of a circle with center near middle of cardiac region.
- b. Interocular teeth eight, inner orbital tooth being bilobed.....*spinimanus* (p. 165).
- bb. Interocular teeth six, inner orbital tooth being entire or notched laterally.
- c. Superoexternal surface of chela with a conspicuous, smooth, silvery, or iridescent area.....*ordwayi* (p. 166).

cc. Superoexternal surface of chela ridged and not iridescent.

d. Last pair of legs with posterodistal margin of merus unarmed; upper margin of dactyl conspicuously fringed with long hairs

depressifrons (p. 163).

dd. Last pair of legs with posterodistal margin of merus armed with spinulose lobe; carpus of cheliped with inner spine greatly elongated

spinicarpus (p. 167).

***Portunus sayi* (Gibbes)**

Figure 144

Lupa sayi Gibbes, 1850, p. 178.

Portunus sayi: Hay and Shore, 1918, p. 428, pl. 33, fig. 2.—Rathbun, 1930a, p. 37, text-figs. 6–7; pl. 14 (rev.).

Recognition characters.—Carapace nearly twice as wide as long, somewhat tumid, smooth and polished to naked eye, finely granulate under magnification. Six frontal teeth including inner orbitals, two submedian teeth smaller but on a line with next pair. External orbital tooth larger than those of anterolateral border except stout, acute ninth; remaining anterolateral teeth blunt and increasing slightly in size posteriorly.

Chelipeds of moderate length, somewhat larger in males than in females; merus with four, rarely three, stout, curved spines in front, none behind; carpus with two spines; hand with an acute spine at articulation and a smaller one near base of movable finger; external surface with two longitudinal ribs with lowermost extending on finger; superior surface with three ribs continuing on finger, innermost one with fringe of hair beneath.

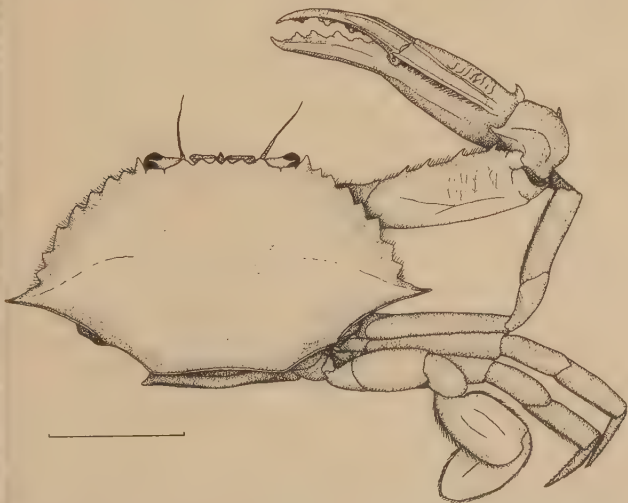


FIGURE 144.—*Portunus sayi* (Gibbes). Animal in dorsal view, legs of left side not shown, 20 mm. indicated.

Measurements.—Carapace: male, length, 27 mm.; width, 53 mm.

Color.—Chocolate brown or purplish with cloudings of olive green or light brown and irregular white or flesh-colored spots; orange margins on spines of chelipeds.

Habitat.—Normally this is a pelagic form living among floating *Sargassum*, but it is often carried into Beaufort Inlet, N.C., by currents.

Known range.—North Atlantic Ocean from Nova Scotia south through Gulf of Mexico to Brazil; mid-Atlantic Ocean; Bermuda; Kerguelen Island, south Indian Ocean.

Remarks.—The species has a fossil record dating from the lower Miocene of North America (Rathbun, 1935).

Ovigerous females are known from April to August in the southeastern United States and in parts of the West Indies. They are also known from Culebra in February and near Nantucket in September (Rathbun, 1930a, in part). Some of the larval stages were described by Lebour (1944) at Bermuda. Coventry (1944) gave new records for the Bahamas in addition to those listed by Rathbun (1930a).

***Portunus anceps* (Saussure)**

Figure 145

Lupea anceps Saussure, 1858, p. 434, pl. 2, figs. 11–11b.

Portunus anceps: Hay and Shore, 1918, p. 431, pl. 33, fig. 8.—Rathbun, 1930a, p. 42, pl. 15 (rev.).

Recognition characters.—Carapace twice as wide as long, pubescent, and with several indistinct, arching, granulate, transverse ridges. Six frontal teeth including inner orbitals, inner orbitals blunt and considerably shorter than outer pair of true frontal teeth, submedian teeth short, smaller than inner orbitals. Anterolateral teeth small, acute, curved forward, last one sharp, slender, and about as long as space occupied by four preceding teeth.

Chelipeds long; merus with four spines in front, a distal one behind; carpus ridged, with a strong internal and a smaller external spine; hand with ridges on outer and superior surfaces, most of ridges continuing on fingers, superointernal ridge more elevated than others, ending distally in two spines, one behind other.

Measurements.—Carapace: male, length, 13 mm., width, 26 mm.; ovigerous female, length, 15 mm., width, 29 mm.

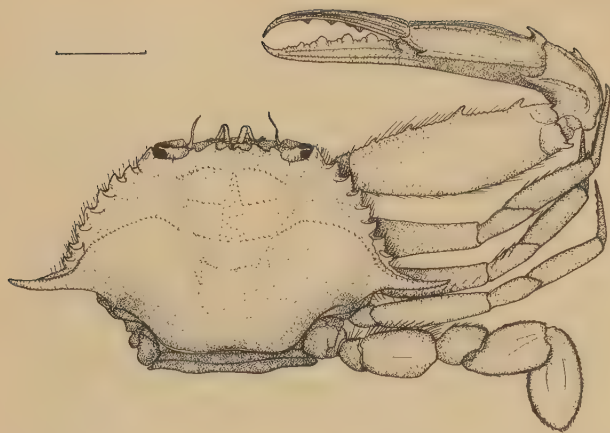


FIGURE 145.—*Portunus anceps* (Saussure). Male in dorsal view, legs of left side not shown, 5 mm. indicated.

Color.—Mottled gray and yellowish white so as to imitate sand; first pair of legs red or yellow; chelipeds and other legs same color in part (Verrill, 1908). Hairs on legs colorless (Abramowitz, 1935).

Habitat.—This form lives on or near sandy shores in tropical waters, but is sometimes carried northward in the Gulf Stream to the North Carolina capes; surface to 40 fathoms.

Type locality.—Cuba.

Known range.—Cape Hatteras, N.C., to Brazil; Bermuda.

Remarks.—Rathbun (1930a) recorded ovigerous females from June in Cuba to October in North Carolina.

***Portunus gibbesii* (Stimpson)**

Figure 146

Lupa gibbesii Stimpson, 1859, p. 57.

Portunus gibbesii: Hay and Shore, 1918, p. 428, pl. 33, fig. 1.—Rathbun, 1930a, p. 49, pls. 16–17 (rev.).

Recognition characters.—Carapace approximately twice as wide as long, not tumid, thickly covered with small spherical granules, pubescent, and with three or four naked, transverse ridges, two of which arise from lateral spines and run toward gastric region. Eight frontal teeth including two points of each inner orbital, median pair of frontal teeth narrower and slightly more advanced than next pair. External orbital tooth not much larger than teeth of anterolateral border, these latter stout, acute, directed forward; last tooth, or lateral spine, slender, sharp, curved forward and about as long as space occupied by three

preceding teeth. One or more small, naked, iridescent areas near anterolateral margin at base of teeth.

Chelipeds long, slender; merus with five to seven spines in front, and one behind at distal end; carpus with a large internal and a smaller external spine; hand slender, ribbed on all surfaces; ribs continued on fingers and roughened by sharp-pointed, appressed tubercles; hand with two spines, one at articulation with carpus, another near distal end of superior rib; fingers nearly straight with incurved tips.

Measurements.—Carapace: male, length, 29 mm.; width, 61 mm.

Color.—Brownish red, transverse ridges on carapace, spines, and margins of chelipeds carmine red; front side of legs brilliantly iridescent by lantern light, iridescence evident to some extent in preserved material.

Habitat.—The species is fairly common about the Beaufort, N.C., region and is often taken in deeper channels of the harbor. Along with *P. spinimanus*, Hildebrand (1955) reported this species as common on the shrimping grounds on Campeche Bank in the Gulf of Mexico, but rare on the Texas coast. Surface to 48 fathoms, rarely deeper.

Type locality.—South Carolina and St. Augustine, Fla.

Known range.—Southern Massachusetts to Texas; Venezuela; Surinam.



FIGURE 146.—*Portunus gibbesii* (Stimpson). Male in dorsal view, legs of left side not shown, 10 mm. indicated.

Remarks.—Ovigerous females have been reported and are otherwise known to occur in the months February to June from North Carolina to Surinam (Holthuis, 1959; Rathbun, 1930a).

Gray (1957) computed gill area per unit weight for *P. gibbesii* as intermediate among a number of swimming crabs studied.

Portunus spinimanus Latreille

Figure 147

Portunus spinimanus Latreille, 1819, p. 47.—Hay and Shore, 1918, p. 429, pl. 33, fig. 4.—Rathbun, 1930a, p. 62, text-fig. 10, pls. 26–28 (rev.).

Recognition characters.—Carapace considerably less than twice as wide as long, finely granulate and pubescent, with a number of prominent, curved, coarsely granulate, transverse ridges. Eight frontal teeth, including inner orbitals, each notched at summit and presenting two points; median pair of teeth slightly narrower and more advanced than next pair, all considerably more advanced than inner orbitals. Outer orbital teeth obtuse, not much larger than teeth of anterolateral borders, these latter strong, acute, or acuminate, about equal in size except last; this tooth about twice as large as others and usually curved forward.

Chelipeds long, pubescent, serratogranulate all over; merus with four, occasionally five, strong, curved spines in front and one at distal end; carpus with two spines, inner one much stronger, and with four conspicuous ridges on upper surface; hand slender, all surfaces with ridges which extend on fingers; a strong spine at carpal articulation and another near base of dactyl; fingers nearly straight, tips incurved.

Measurements.—Carapace: female, length, 55 mm.; width, 88 mm.

Variations.—Large males have relatively longer, thinner chelipeds and longer walking legs than large females.

Color.—Pubescence yellowish or reddish brown, ridges of carapace, spines of chelipeds, fingers and tips of legs reddish brown; anterolateral teeth reddish at base, white at tips; merus, carpus, and hand of chelipeds with white blotches.

Habitat.—This species is common in the waters off Beaufort Inlet, N.C., and is sometimes found in deeper channels of the harbor. *P. gibbesii* is



FIGURE 147.—*Portunus spinimanus* Latreille. Male in dorsal view, legs of left side not shown, 20 mm. indicated.

often found in company with *P. spinimanus*. A similar association of these two species was reported by Hildebrand (1955) for the Campeche Banks in the Gulf of Mexico where they are common. On beach under *Sargassum*; surface to 50 fathoms.

Type locality.—American waters, common in Brazil.

Known range.—New Jersey through Gulf of Mexico and West Indies to southern Brazil; Bermuda.

Remarks.—This species, which somewhat resembles *P. gibbesii*, can be readily distinguished from the latter by its narrower, rounder form, and by the entire lack of iridescent patches on the carapace mentioned for *P. gibbesii*.

Ovigerous females are known from January to July in Florida (Wass, 1955, in part); March in Campeche; April in Isle of Pines; May, August, and September in Surinam (Holthuis, 1959); and July in St. Thomas, V.I. (Rathbun, 1930a). Lebour (1950) found an ovigerous female among *Sargassum* in Bermuda in May, and from the eggs reared larvae which she illustrated.

Gray (1957) computed gill area per unit weight for *P. spinimanus* as intermediate among a number of swimming crabs studied.

***Portunus ordwayi* (Stimpson)**

Figure 148

Achelous ordwayi Stimpson, 1860a, p. 224.
Portunus ordwayi: Hay and Shore, 1918, p. 431, pl. 33, fig. 6.—
Rathbun, 1930a, p. 71, pl. 33 (rev.).

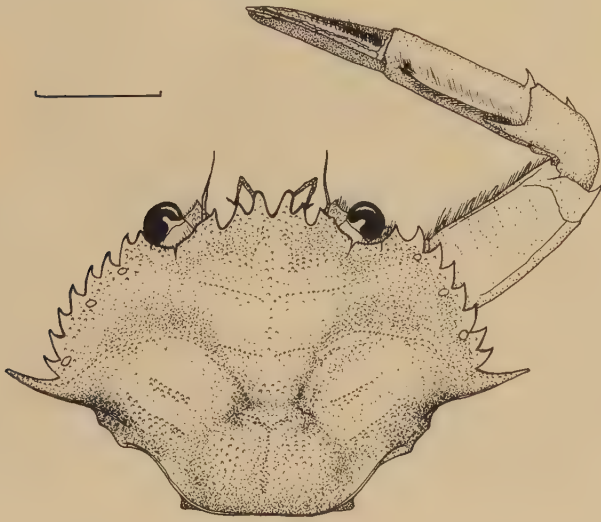


FIGURE 148.—*Portunus ordwayi* (Stimpson). Male in dorsal view, legs not shown except for right cheliped, 10 mm. indicated.

Recognition characters.—Carapace approximately 1.5 times as wide as long, uneven, elevations granulate and depressions pubescent, with a number of conspicuous, curving, transverse ridges. Six frontal teeth including acuminate inner orbitals; true frontal teeth about equal in size, triangular, acute, middle pair advanced beyond others. Outer orbital tooth large; antero-lateral teeth diminishing slightly in size from first to seventh, inclusive, eighth about as long as space occupied by two preceding teeth, tips of all acute and turned forward.

Chelipeds of moderate length; merus with four or five strong spines in front, a single distal one behind; carpus ribbed and with strong internal and much smaller external spine; hand ribbed on all surfaces except flat, highly iridescent, superior surface; superointernal ridge raised into a crest terminating distally in a sharp spine. Margins of carapace and chelipeds more or less fringed with silky hairs.

Measurements.—Carapace: male, length, 26 mm.; width, 42 mm.

Color.—Carapace and legs reddish brown due to fine mottling with red, yellowish brown, and

gray; pale orange beneath, deeper orange on chelipeds and legs; chelae deep red brown above, fingers with two cross bands of light orange red. Blue coloration also apparent near red and dark pigments; hairs on appendages deep red (Abramowitz, 1935).

Habitat.—This is another of the tropical swimming crabs which move northward with warm water currents; surface to 58 fathoms, rarely deeper.

Type localities.—Key Biscayne and Tortugas, Fla.; St. Thomas, [V.I.].

Known range.—Vineyard Sound, Mass.; North Carolina through Gulf of Mexico, Caribbean Sea, and West Indies to State of Bahia, Brazil; Bermuda.

Remarks.—Rathbun (1930a) listed an ovigerous female in March from Florida.

***Portunus depressifrons* (Stimpson)**

Figure 149

Amphitrite depressifrons Stimpson, 1859, p. 58.
Portunus depressifrons: Hay and Shore, 1918, p. 430, pl. 33, fig. 7.—Rathbun, 1930a, p. 84, pl. 41 (rev.).

Recognition characters.—Carapace approximately 1.6 times as wide as long, uneven, pubescent, and with indistinct transverse ridges. Six frontal teeth, including inner orbitals much larger than others, tips of all teeth about on a line. External orbital tooth strong, tip rounded; antero-lateral teeth acute, turned forward, lateral tooth scarcely longer than one in front, teeth and intervals between them fringed with hairs.

Chelipeds trigonal, serratogranulate and pubescent; merus with five spines in front and a distal one behind; carpus with two spines, outer much smaller than inner one; hand short and compressed, upper margin raised into a crest terminating distally in a stout spine, a smaller spine at carpal articulation; fingers flattened, dactyl with border of hairs on superior margin. Walking legs unusually long and slender, first pair with articles fringed with hairs. Swimming legs shorter than in most species of genus.

Measurements.—Carapace: male, length, 26 mm.; width, 41 mm.

Color.—Carapace in life irregularly mottled with light and dark gray, closely imitating colors of sand; chelipeds and posterior legs similar, though paler; first pair of walking legs bright

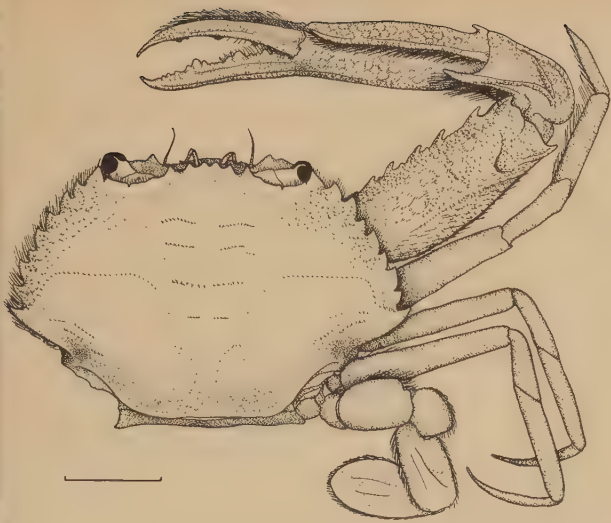


FIGURE 149.—*Portunus depressifrons* Stimpson. Male in dorsal view, legs of left side not shown, 10 mm. indicated.

purple, or deep blue in larger specimens, while some portion of same color usually apparent on next two pairs, but color of first pair in striking contrast with rest of crab. Very young specimens do not show this distinction in color of legs, so far as observed (Verrill, 1908).

Habitat.—Abundant in shallow water on sandy bottoms of coves and inlets at Bermuda (Verrill, 1908); surface to 16 fathoms.

Type localities.—South Carolina and Florida Keys.

Known range.—Fort Macon, N.C. (Coues and Yarrow, 1878; Kingsley, 1880) to Gulf of Campeche and Caribbean Sea; Bermuda.

Remarks.—This crab has not been collected in the Carolinas for many years, so far as recorded. Records in the U.S. National Museum show no specimens from farther north than Key West, Fla., and the Bahamas near the southeast coast of the United States. A number of specimens in the U.S. National Museum collection were taken from the stomachs of the gray snapper, *Lutjanus* (= *Neomaenus*) *griseus*, the yellow goatfish, *Mulloidichthys* (= *Upeneus*) *martinicus*, and other predaceous fish. Rathbun (1930a) reported ovigerous females in June from Florida, and in August from Florida and the Caribbean. More recently, egg-bearing females have been taken on Campeche Banks in late August.

Portunus spinicarpus (Stimpson)

Figure 150

Achelous spinicarpus Stimpson, 1871a, p. 148.

Portunus spinicarpus: Hay and Shore, 1918, p. 429, pl. 33, fig. 3.—Rathbun, 1930a, p. 92, pl. 45.

Recognition characters.—Carapace slightly more than twice as wide as long, sculptured, with a number of naked, rather coarsely granulate, arching, transverse ridges separated by finely granulate and pubescent surfaces. Six frontal teeth, including inner orbitals, with sinuate but unnotched outer margins; true frontal teeth narrow, acute, separated by broad notches, median pair considerably advanced beyond others. External orbital tooth acute, larger than neighboring teeth of anterolateral margin; latter varying somewhat in size, concave sided, acute; lateral tooth with form of slender curving spine more than half as long as anterolateral border; posterolateral angle sharp, margin slightly recurved.

Chelipeds long, slender; merus with four or five stout, curved spines in front, and a single, similar, distal spine behind. Carpus with two spines, outer one small and weak, inner one long, extending along side of hand to near base of dactyl. Hand with serratotuberculate ridges, prolonged on fingers, and two spines, one at carpal articulation, another near base of movable finger. Fingers nearly straight, incurved at tips.

Measurements.—Carapace: male, length, 18 mm.; width, 38 mm.

Variations.—Rathbun (1930a) stated that ovigerous females are smaller than males, and their chelipeds are shorter, with the carpal spine not reaching beyond the superior spine of the hand. The lateral spine is relatively longer in young than in old individuals and changes in angle of projection with age, extending straight laterally or slightly backward in the young, but curving slightly forward in mature individuals.

Color.—Carapace buff pink, mottled, highest ridges touched with cinnamon red; fingers bordered with crimson and maroon; two basal teeth of dactyl and margin of palm white; rest of chela maroon purple and purplish red, same color on fringe of hair on carpal spine; walking legs purple. (Schmitt in Rathbun, 1930a, where great detail on younger individuals is given.)

Lupa hastata Say, 1817, p. 65.
Callinectes sapidus Rathbun, 1896a, p. 352, pls. 12; 24, fig. 1; 25, fig. 1; 26, fig. 1; 27, fig. 1 (rev.).—Hay and Shore, 1918, p. 432, pl. 35, fig. 1.—Rathbun, 1930a, p. 99, pl. 47 (rev.).

Recognition characters.—Carapace, including lateral spines, 2.5 times as wide as long, moderately convex, nearly smooth, except lightly tuberculate on inner branchial and cardiac regions; a tuberculate transverse line from side to side between lateral spines, and a shorter transverse line about halfway between this and frontal margin. Four frontal teeth, including inner orbitals, triangular, acute, both pairs more or less distinctly bilobed. Anterior eight anterolateral spines of subequal length, concave on both margins and acuminate; lateral spines nearly straight, usually longer than space occupied by three preceding teeth; inner suborbital tooth prominent and acute.

Chelipeds of male large and powerful, smaller in female; merus with three spines in front and one small spine at distal end behind; carpus with one spine and one spiniform tubercle on external surface; hand strong, prominently ribbed, and with a strong proximal spine; fingers nearly straight and strongly toothed. Abdomen of male in form of inverted T; basal segments broad, distal segments narrow; penultimate segment constricted in proximal half, wider at both ends, terminal segment approximately oblong-lanceolate; first pleopods reaching nearly to, or beyond, extremity of abdomen, approximated through basal half, distal portions widely divergent except at tips. Immature female with abdomen triangular; mature female with abdomen broad, rounded, and lying loosely on ventral side of thoracic sterna.

Measurements.—Width of carapace (including spines): males, 200 mm.; females, 198 mm.; smallest mature females (excluding dwarfs), 86 mm. Exceptional males in water of low salinity may measure 230 mm., or more, in width.

Color.—Grayish, or bluish green of varying shades and tints, relieved by more or less red on spines of carapace; males with blue fingers on hands, mature females with red fingers on hands; underparts off white with tints of yellow and pink. Churchill (1919) gave a colored frontispiece showing ventral and other views.

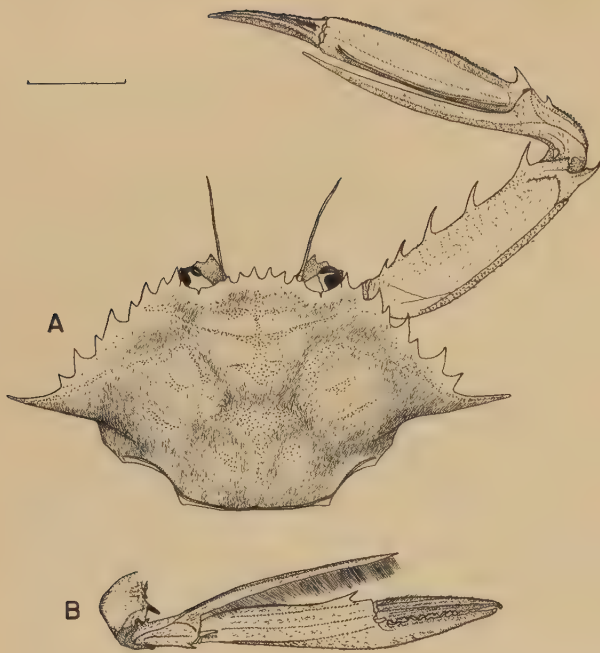


FIGURE 150.—*Portunus spinicarpus* (Stimpson). A, male in dorsal view, legs not shown except for right cheliped; B, right chela of male in frontal view; 5 mm. indicated.

Habitat.—This appears to be a species living in deeper waters of the region. On shrimp grounds in the western Gulf of Mexico, Hildebrand (1954) reported it as found only along the seaward side in depths of 15 to 37 fathoms. Five to 300 fathoms.

Type localities.—Off Tortugas, Carysfort Reef, Conch Reef, Alligator Reef, Pacific Reef, and American Shoal, Fla.; lat. 31°31' N. long. 79° 41' W. off Georgia; in depths ranging from 13 to 150 fathoms.

Known range.—Off Cape Hatteras, N.C., to State of São Paulo, Brazil.

Remarks.—Ovigerous females have been taken from January to September from Florida to Surinam, and in November in Texas. Pearse (1932b) found the barnacle, *Dichelastis sinvata* Aurivillius, on a number of individuals.

Genus *Callinectes* Stimpson, 1860

Rathbun, 1930a, p. 98.

KEY TO SPECIES IN THE CAROLINAS

- a. Frontal teeth, including inner orbitals, four
sapidus (p. 168).
- aa. Frontal teeth, including inner orbitals, six
ornatus (p. 172).

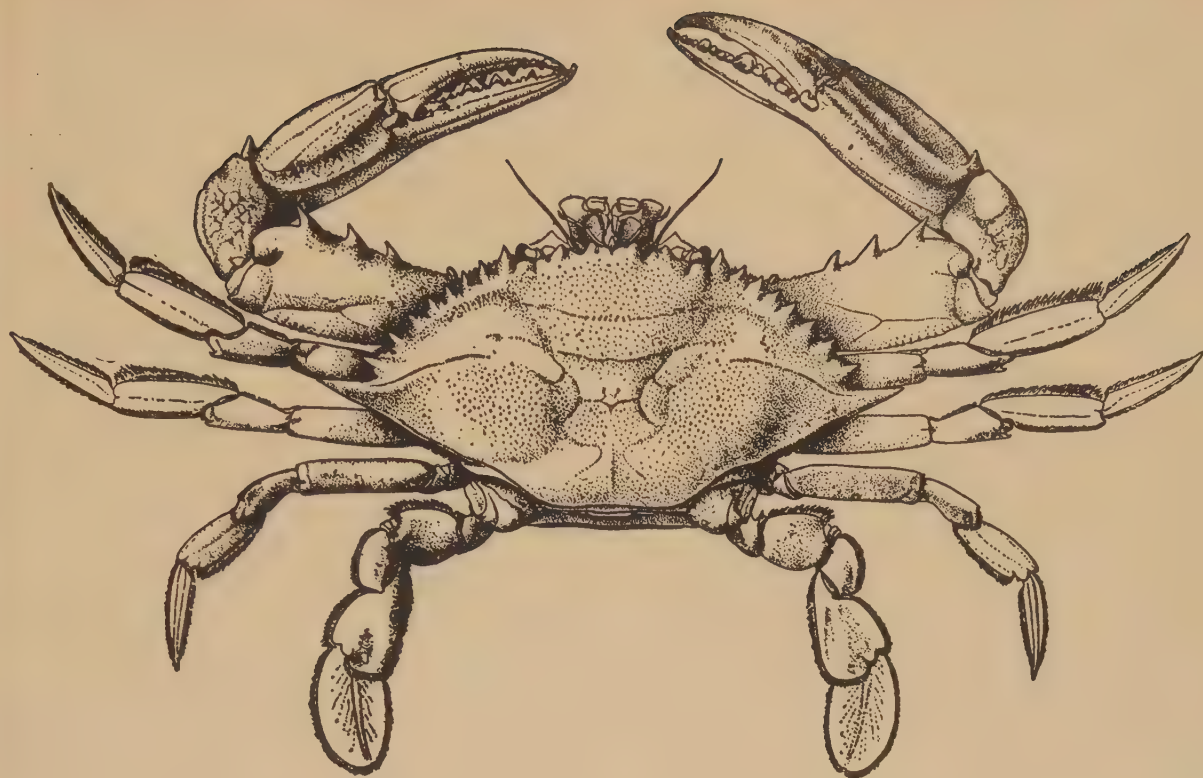


FIGURE 151.—*Callinectes sapidus* Rathbun. Animal in dorsal view (after Rathbun, 1884).

Habitat.—Found on a variety of bottom types in estuaries and shallow oceanic water; water's edge to 20 fathoms.

Type locality.—[East coast of United States].

Known range.—Native recent range, Nova Scotia (no longer endemic, Bousfield, personal communication) to Uruguay; Bermuda. The species has been introduced in Europe, and was reported from southwest France in 1901; from Holland in 1932, 1934, and 1951; near Copenhagen, Denmark, in 1951; in and near Venice, Italy, in 1949 and 1950; and in Israel in 1955. Holthuis (1961) reviewed these occurrences in addition to recently found well-established colonies in Turkey and Greece and remarked that the species must now be regarded as indigenous to Europe.

Remarks.—There is a tremendous literature concerning the blue crab, largely because of its great economic value. Since it is not possible to summarize this literature in a brief account such as this, the interested student is referred to the comprehensive bibliography compiled by Cronin, Van Engel, Cargo, and Wojcik (1957) for a list of the literature to that date, to excellent life history

and ecological summaries by Churchill (1919), Truitt (1939), and Van Engel (1958) for the crab in Chesapeake Bay; and to Darnell (1959) for occurrence in Louisiana. Though these papers are current and available, for the sake of convenience certain essentials are reviewed here.

The fossil record for *Callinectes sapidus* reaches back to the lower Miocene of Florida, and the species has been found at later levels in Virginia, Massachusetts, New Jersey, and the Carolinas (Rathbun, 1935; Blake, 1953).

The spawning season on the east coast of the United States is quite long. Females with yellow egg masses attached have been found in North Carolina from as early as March 21 to as late as October 26. In that area, the greatest number of females with eggs occur in spring, the time of peak occurrence varying somewhat with season. In Chesapeake Bay, the spawning season, with rare exceptions, extends from late April to early September with the peak occurring in June. Farther south, on the coast of Texas the spawning season extends from December to October and may include November as well, but the peak oc-

curs in June and early July (Daugherty, 1952). Five stages in the reproductive cycle of mature females have been described (Hard, 1942), and a number of authors have shown that the number of eggs in an egg mass (sponge) may range from 700,000 to more than 2 million.

The eggs hatch into zoeae, undergoing development through seven stages. These stages have been described from laboratory cultures (Costlow, Rees, and Bookhout, 1959; Costlow and Bookhout, 1959). Atypically, an eighth stage may occur. The last zoeal stage molts into a megalops stage and this into the first crab stage.

Churchill found that eggs hatch in about 15 days at 26.1° C. and slightly faster at higher temperatures. Development from hatching to megalops lasts from 31 to a maximum of 49 days in various salinities, but development time in the different stages is quite variable even in a single salinity-temperature combination. The megalops stage lasts from 6 to 20 days. It was found that development progresses at a comparable rate in salinities between 20.1 and 31.1 ‰ at 25° C. Salinity above 31.1 ‰ slowed development, and below 20.1 ‰ larvae rarely completed the first molt. Larvae never went beyond the first zoeal stage when reared at 20° C. and did not progress beyond the third zoeal stage when reared at 30° C. Once the first crab stage is reached, the animals continue to molt as they grow and are estimated to undergo some 18 to 20 or more molts before reaching maturity (Van Engel, 1958).

In Chesapeake Bay, where the crab is perhaps more abundant than in other areas, it has been demonstrated that crabs spawned in June of one year are mature about 14 months later and at that time mate. Most mating pairs are found in July, August, or September, though the mating season extends from May to October. At this time, females ready to molt into the mature stage (terminal molt) are carried about, cradled upright, under the males' bodies. Such pairs are called doublers. The male frees the female during the time she is actually casting the old exoskeleton, but when this is shed he grasps her again, this time with the ventral surfaces together, and completes the breeding act by introducing sperm via the copulatory stylets into the spermathecae. Copulation may last for several hours. When

sperm transfer is complete, the female is allowed to resume an upright posture and is again carried under the male for a time until her shell is hardened. Males may mate more than once and at any time during their last three intermolts (Van Engel, 1958); females only do so once, but the sperm supply may serve to fertilize more than one mass of eggs. Usually, a female mated in late summer casts the first batch of eggs the following spring at an age of approximately 2 years, but egg laying may be at any time from 2 to 9 months after mating. A second spawning has been observed to occur later in summer among some individuals, and it is possible that a third may occur, possibly as late as the succeeding spring or at an age of 3 years. Three years is judged to be about the normal maximum age for this species.

The life history of the blue crab is complicated by the fact that it leads a migratory existence. The migratory patterns have been studied in greatest detail in Chesapeake Bay but the same pattern appears to be true of other areas as well. Mating usually takes place in water of reduced salinity well up in estuaries. After this, the females migrate downstream to areas of higher salinity near the mouths of estuaries where the eggs are laid and hatched, whereas the males tend to remain in the low-salinity areas for the remainder of their lives. For this reason, samples of adult crabs (or commercial catches) near the sea contain greater numbers of females, whereas those from the middle or upper reaches of bays contain larger percentages of males except at the breeding season. Once in the spawning areas, the females tend to remain there for the remainder of their lives or move a short way out to sea. Once hatched, the zoeae lead a planktonic existence until they transform to the megalops stage. As soon as the crabs transform to the first crab stage, they begin a migration up the estuary toward the mating grounds. Some early recruits may reach these areas in their first summer of life, the remainder early in the second year of life. In areas smaller than Chesapeake Bay, there may be a certain amount of overlap in mating and spawning grounds but the two areas tend to be distinct. In Chesapeake Bay, the spawning grounds are near the mouth of the Bay; in North Carolina and Louisiana, near the inlets and passes. In Texas,

most females with eggs are found in the Gulf proper (Daugherty, 1952).

Aside from size variation associated with the annual growth cycle, there is an apparent variation in size correlated with location in which the animals are found (Van Engel, 1958). Though never conclusively proved by experiments, it is thought that there is a negative correlation of size with the salinity in which a crab matures. Very large males are probably large because they have remained in water of low salinity. Fischler (1959) reviewed the occurrence of "dwarf" ovigerous females ranging in width from 52.3 to 80 mm. All these specimens were taken near the sea, and, as the author pointed out, may be small because of environmental influences of high salinities throughout life.

That the blue crab can tolerate fresh water is well established. The subject is reviewed in some detail by Odum (1953). On the basis of experiment and observation he reached the conclusion that oligohaline (100–1,000 p.p.m. Cl) and nearly oligohaline waters (25–100 p.p.m. Cl) can be invaded to a considerable extent if the crabs are able to adjust slowly to the reduced chlorinity, which, of course, is the case in natural invasions. Many of the Florida streams and lakes are oligohaline and contain blue crabs, but in other areas this is not true and blue crabs in such areas are seldom found far from salt water.

Because the blue crab supports the largest crab fishery in the United States, fluctuations in abundance (especially in the Chesapeake area) have been the subject of many conjectures and a number of investigations. Pearson (1948) dealt with this subject at length. The fluctuations appear to be associated with variable rates of survival in the first year of life. No correlation was found between relative abundance of female crabs and their progeny. On the basis of examination of 13 generations, size of spawning stock did not determine size of population surviving to commercial age at the rate of fishing prevailing during the years studied. Pearson found evidence that excessively cold weather may reduce availability of immature and adult crabs either by direct mortality or by making crabs less available to the fishery immediately after the periods of cold weather. Heavy runoff in some wet years may lower salinity in the spawning areas enough to have an ad-

verse effect on survival of young, but such limits are poorly understood.

Piers (1923) reported a population of blue crabs in Nova Scotia, the recorded northern limit for the species, and considered that it was a natural rather than an introduced population. Bousfield (personal communication) reports that the species is certainly no longer endemic there. Scattergood (1960) commented that fluctuations in the population in Maine seemingly were correlated with temperature when a series of warm years accompanied an increase in number of blue crabs.

The blue crab is often summarily dismissed as a scavenger. Though it may be a scavenger, and, indeed, is lured to crab pots or wire traps by means of dead fish used for bait, students of the feeding habits of the species agree that it is an omnivore and prefers fresh to putrid flesh (Churchill, 1919; Truitt, 1939; Van Engel, 1958). Darnell (1961) showed that blue crabs in Lake Pontchartrain, La., eat a variety of materials including fishes, large and small bottom animals, some vascular plant material, and organic detritus. Of these materials, the category including small bottom animals (*e.g.*, those that are intimately associated with the bottom) made up about half of the diet. There are numerous notes on feeding and predation in the literature recording such habits as feeding on oysters, clams, and tunicates.

In a study of gill area correlated with degree of activity and habit of several species of crabs, Gray (1957) found that the blue crab has a larger gill area per gram of body weight than the other portunids studied (*Ovalipes*, *Arenaeus*, and *Portunus* spp.) and, in fact, exceeded that of any crab studied among aquatic, intertidal, and land crabs in the Beaufort, N.C., area. The blue crab is noted for its vigorous and pugnacious nature, and this anatomical feature gives one reason for such temperament.

Callinectes sapidus is fairly long-lived following its last molt, and thus affords a lodging place for barnacles and bryozoans. Its gills and gill chambers become clogged with clusters of a small stalked barnacle, *Octolasmus lowei* (Causey, 1961). The barnacles *Balanus amphitrite* and *Chelonibia patula* attach to the carapace. The sacculinid parasite, *Lowothyllacus texanus*, lives

beneath the abdomen (Wass, 1955). Hopkins (1947) discussed infestations of the parasitic nemertean *Carcinonemertes carcinophila* on female blue crabs showing that only light-colored worms are found in the gills of mature females which have never spawned. Large red worms are found only on the gills of mature female crabs which have spawned at least once, or in the gills and egg masses of ovigerous females. Presence of large red nemerteans in the gills is a sure sign that the crab has spawned some time in the past. Pearse (1932b) reported trematode metacercariae on the gills.

Pigment in the melanophores of *C. sapidus* displays an endogenous rhythm with a frequency of 24 hours in the Gulf of Mexico where there is one high and one low tide per day (Fingerman, 1955). The pigment is in a dispersed state during the day and in a contracted state at night. This cycle is maintained under constant laboratory conditions. Superimposed on the diurnal rhythm is a tidal rhythm with a frequency of 12.4 hours. This rhythm is manifested by a supplementary dispersion of melanin which occurs about 50 minutes later each day and is most evident when the low or high tide is either in the morning or late afternoon. Under constant conditions, the phases bear a definite relationship to times of low and high tides in the native habitat. Also, there is evidence for a semilunar rhythm. Only once every 14.8 days are the diurnal and tidal rhythms in the same phases relative to each other.

Callinectes ornatus Ordway

Figure 152

Callinectes ornatus Ordway, 1863, p. 571.—Hay and Shore, 1918, p. 433, pl. 34, fig. 2.—Rathbun, 1930a, p. 114, pl. 50 (rev.).

Recognition characters.—Carapace, including lateral spines, slightly more than twice as wide as long, somewhat tumid, finely granulate throughout, transverse lines distinct, metagastric area less than half as long as its anterior width. Six frontal teeth including inner orbitals, submedial teeth short, variable in length. Anterolateral teeth shallow and broad, tips of first five or six acute, others acuminate; lateral spines curved forward, scarcely as long as space occupied by three preceding teeth; inner suborbital angle prominent.

Chelipeds shaped as in *C. sapidus*, but smaller, with spines possibly more acute; ridges of hand

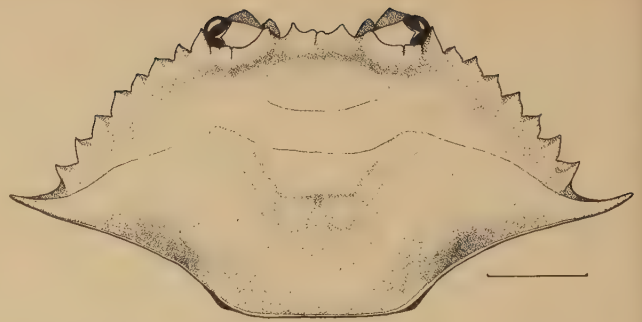


FIGURE 152.—*Callinectes ornatus* Ordway. Animal in dorsal view, legs not shown, 10 mm. indicated.

more developed, and teeth on fingers relatively larger and sharper. Abdomen of male with first segment produced laterally into an acute, up-turned spine.

Measurements.—Carapace: male, length, 33 mm.; width, 74 mm.

Color.—Adult male: Carapace green dorsally, irregular areas of iridescence at bases of, and between, anterolateral teeth, and on posterior and posterolateral borders. Chelipeds and portions of legs similar in color or more tannish green dorsally, with iridescent areas on outer and upper edges of carpus and hands; chelae white on outer face, blue to fuchsia on inner surface, with fuchsia on tips of fingers and teeth of opposed edges. Lateral spines and some anterolateral teeth, as well as spines on chelipeds, white tipped. Walking legs grading from fuchsia distally through violet blue to light blue mottled with white proximally, pubescence on legs beige. Swimming legs variably mottled with white; all legs with stellate fuchsia markings at articulations. Under parts white and blue.

Ovigerous female: similar to male except with more violet blue on inner surface of chelae; fingers either with white teeth or fuchsia-colored teeth. Legs with dactyls reddish orange grading abruptly to blue on propodi, pubescence brown to beige. Abdomen with iridescent areas.

Habitat.—This crab, like its near relative, *C. sapidus*, is a coastal species often found in estuaries, sometimes in fresh water. Brues (1927) observed a large, active male that had been trapped at the head of a Cuban tidal river in fresh water during a dry period of about 3 months' duration. Lunz (1958), writing of a form from the South Carolina crab fishery,

doubtfully referred to *C. ornatus*, said that it tends to occupy oceanic waters and high- to medium-salinity areas of estuaries chiefly in a temperature range of 15° to 31° C., but has been found in temperatures as low as 9° C. From over 500 trawl hauls in South Carolina, a depth maximum of 9 fathoms was found for the species. However, specimens have been taken under a light at night swimming at the surface in 925-fathom water off the Mississippi River Delta (U.S. National Museum notes).

Reported from surface to 40 fathoms, with above exception.

Type localities.—Charleston Harbor [S.C.]; Tortugas [Fla.]; Bahama Islands; Gonaives [Haiti]; Cumana [Venezuela].

Known range.—New Jersey to State of São Paulo, Brazil; Bermuda.

Remarks.—Blake (1953) reported a fossil record for this species dating from the Pleistocene of Maryland. Lunz (1958), in addition to habitat data, reported ovigerous females from South Carolina in May, August, and September, and added that spawning probably takes place offshore. He found a sex ratio of approximately two males to one female. Ovigerous females occur as late as November in North Carolina.

Genus *Arenaeus* Dana, 1851

Rathbun, 1930a, p. 134.—Hemming, 1958b, p. 13.

Arenaeus cribrarius (Lamarck). Speckled crab

Figure 153

Portunus cribrarius Lamarck, 1818, p. 259.

Arenaeus cribrarius: Hay and Shore, 1918, p. 434, pl. 34, fig. 3.—Rathbun, 1930a, p. 134, pl. 58, figs. 2–3; pls. 59–60 (rev.).

Recognition characters.—Carapace more than twice as wide as long, finely granulate, produced on each side into a strong spine. Front not so far advanced as outer orbital angles, with six teeth including inner orbitals; central tooth of each side partly coalesced with adjacent submedian tooth. Anterolateral teeth strong, somewhat acuminate, heavily ciliate beneath. Superior wall of orbit with two deep fissures dividing it into three lobes; inferior wall of orbit with wide external fissure and inner angle much advanced; lower surface of carapace hairy.

Chelipeds of moderate size; merus with three spines on anterior border, and a short tuberculi-form one near distal end of posterior border;

carpus with two spines; hand short, with five longitudinal granulose ridges and two spines, one at articulation with carpus, another above base of dactyl. Walking legs rather short and broad, densely ciliate. Swimming legs stout. Basal segment of abdomen produced on each side into strong, sharp, slightly upcurved spine.

Measurements.—Carapace: male, length, 48 mm.; width, 116 mm.

Color.—Light vinaceous brown or olive brown thickly covered over dorsal surface with small, rounded, white spots; spots on dorsal surface of chelipeds somewhat larger; tips of walking legs yellow. Color pattern persisting in alcohol.

Habitat.—As far as known, this crab seldom enters estuaries and is rarely washed ashore along the outer beaches. It lives in rather shallow water close to the shore, and is well adapted to life in the waves and shifting sand. Hildebrand (1954) reported it as preferring the relatively shallow water of the white shrimp grounds in Texas. Siebenaler (1952) reported it as a "trash" form on the Florida east coast shrimp grounds. Waterline along beaches to 37 fathoms.

Type locality.—Brazil.

Known range.—Vineyard Sound, Mass., to State of Santa Catarina, Brazil.

Remarks.—Ovigerous females are known in August from Florida, and in September from Venezuela and Brazil.



FIGURE 153.—*Arenaeus cribrarius* (Lamarck). Male in dorsal view, legs not shown except for right cheliped, color pattern of right side indicated, 50 mm. indicated.

Pearse, Humm, and Wharton (1942) stated that where waves roll at the low-tide mark *A. cribrarius* may scurry across sand and burrow backward. In doing this, the crab flirts sand forward away from the body with the chelipeds, waves legs two to four rapidly from the median line laterally, and moves the fifth legs posteriorly and dorsally, thus sinking vertically into the sand. Often the crabs bury themselves completely. The heavy coat of hairlike setae on each side of the mouth parts keeps out sand, and with the chelipeds held close to the body a clear channel is left for currents from the branchial chamber. Ability to maintain strenuous activity in the breaker zone near shore may be partially explained also by the relatively large respiratory surface in this species (Gray, 1957).

Genus *Cronius* Stimpson, 1860

Rathbun, 1930a, p. 138.

Cronius ruber (Lamarck)

Figure 154

Portunus ruber Lamarck, 1818, p. 260.

Cronius ruber: Rathbun, 1930a, p. 139, pls. 62-63 (rev.).

Recognition characters.—Carapace hexagonal, smooth, pubescent; a sinuous transverse ridge extending between lateral spines, and another

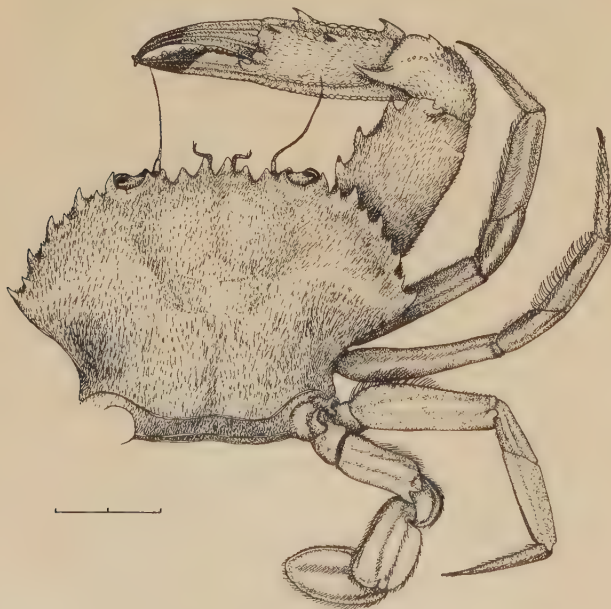


FIGURE 154.—*Cronius ruber* (Lamarck). Animal in dorsal view, legs of left side not shown; (redrawn from Monod, 1956).

shorter, transverse, biarcuate ridge about halfway between this ridge and front. Front proper with four teeth, not including inner orbitals; submedian pair of teeth most advanced; second pair more pointed, and directed slightly laterad, separated from notched inner orbitals by a deep cut. Orbit nearly circular. Basal article of antenna with spine below insertion of movable portion. Anterolateral teeth unequal, alternating large and small; lateral spine not strikingly enlarged.

Chelipeds heavy; merus with four to six spines in front, and with small distal spine behind; carpus with granulate ridges, one large internal spine, and three small spines on outer surface; hand with granulate ridges on all surfaces, armed with four spines on superior surface, two on inner and two on outer border.

Measurements.—Carapace: male, length, 50 mm.; width, 75 mm.

Color.—"Violet red or deep purple red more or less marbled with a lighter shade or white. Extremity of all spines black." (Rathbun, 1930a.)

Habitat.—Siebenaler (1952) reported *C. ruber* as a "trash" form on the Tortugas shrimping grounds; below low tide mark to 40 fathoms.

Type locality.—Brazil.

Known range.—South Carolina to State of Santa Catarina, Brazil; Lower California, Mexico, to Peru and Galapagos Islands; west Africa from Senegal to Angola.

Remarks.—Rathbun (1930a) reported ovigerous females from May through September in Curaçao, in June from Cuba, and in July from Jamaica.

Family Cancridae

Carapace broadly oval or hexagonal. Last pair of legs not adapted for swimming. Antennules folding lengthwise. Antennae with flagella more or less hairy.

Genus *Cancer* Linnaeus, 1758

Rathbun, 1930a, p. 176.—Hemming, 1958b, p. 51.

MacKay (1943) gave a review of the modern world distribution of members of the genus *Cancer*, as well as the geologic record which dates from the Eocene Period. The modern distribution of the genus is limited, apparently by temperature, to the temperate zones except along the northwestern coast of South America in the cold Humboldt Current.

KEY TO SPECIES IN THE CAROLINAS

- a. Anterolateral teeth of carapace with margins granulate; chelipeds granulate, not denticulate
irroratus (p. 175).
- aa. Anterolateral teeth of carapace with denticulate margins; upper margin of palm denticulate
borealis (p. 175).

Cancer irroratus Say. Rock crab

Figure 155

Cancer irroratus Say (in part), 1817, p. 59, pl. 4, fig. 2.—Hay and Shore, 1918, p. 435, pl. 35, fig. 1.—Rathbun, 1930a, p. 180, text-fig. 29, pl. 85, fig. 1 (rev.).

Recognition characters.—Carapace approximately two-thirds as long as wide, convex, granulated. Anterolateral border divided into nine teeth with margins granulate, not denticulate as in *C. borealis*, and with notches between teeth continued on carapace as short, closed fissures giving teeth a pentagonal character. Posterolateral border a granulated ridge with one tooth at outer end similar to those of anterolateral border but smaller. Front with three teeth, middle one exceeding others and depressed.

Chelipeds of moderate size, not so long as second pair of legs; carpus with granulated ridges and a sharp spine at inner distal angle; hand nearly smooth on inner face, outer face with four or five granulated lines, two lower ones continued on slightly deflexed immovable finger, superior one cristate. Walking legs rather long and slender; merus of first and second pairs extending far beyond carapace. Abdomen of male broad, first, second, and third segments with transverse granulated ridge.

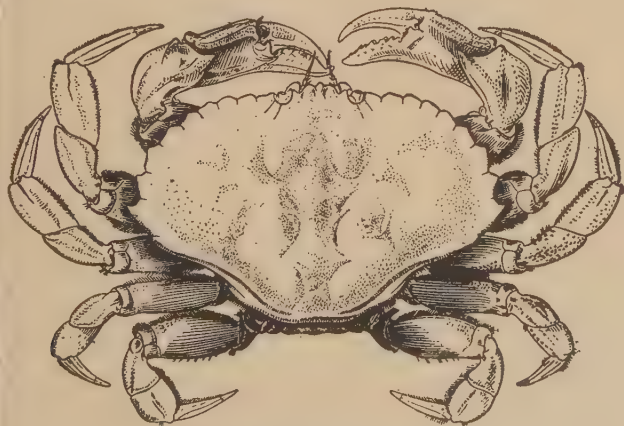


FIGURE 155.—*Cancer irroratus* Say. Male in dorsal view, reduced (after Rathbun, 1884).

Measurements.—Carapace: length, 65 mm.; width, 95 mm.

Color.—Yellowish closely dotted with dark purplish brown, becoming reddish brown after death.

Habitat.—Most individuals taken near Beaufort, N.C., are immature, but larger specimens have been taken farther from the coast. This species, and the following one, are members of a northern fauna with ranges extending south of the Carolinas only in deep water. Low water mark to 314 fathoms.

Type locality.—“Inhabits the ocean.” [Atlantic coast of United States.]

Known range.—Labrador to South Carolina; shallow water in the North, deeper water in the South.

Remarks.—This species has a fossil record extending from the Miocene to the present in North America (MacKay, 1943). Ovigerous females are known to occur in March in Florida, and have been reported in August from Massachusetts (Rathbun, 1930a).

Cancer borealis Stimpson. Jonah crab; northern crab

Figure 156

Cancer borealis Stimpson, 1859, p. 50.—Hay and Shore, 1918, p. 434, pl. 35, fig. 2.—Rathbun, 1930a, p. 182, text-fig. 30 (rev.).

Recognition characters.—Carapace transversely oblong, approximately two-thirds as long as wide, angular at sides, surface granulate. Anterolateral margins divided into nine quadrangular, crenate lobes or teeth, with margins minutely denticulate and with notches between teeth continued on carapace as short closed fissures. Front produced beyond internal orbital teeth and provided with three teeth, center one longest and depressed. Orbits circular, with two narrow fissures above and two below; suborbital lobe strongly produced.

Chelipeds nearly as long as second pair of legs, stout; carpus and hand with strong, granulose rugae; carpus with sharp spine at inner angle; hand smooth on inner face, heavily rugose on outer face, two rugae continued from hand on slightly deflexed immovable finger; dactyl with rough upper surface, both fingers slaty black at tip. Walking legs short, fringed beneath, dactyls dark tipped.

Measurements.—Carapace: length, 62 mm.; width, 91 mm.



FIGURE 156.—*Cancer borealis* Stimpson. Male in dorsal view, reduced (after Smith, 1879).

Color.—Yellowish beneath, red above; back with two curved lines of yellowish spots and, behind middle, a figure somewhat resembling letter H; legs mottled and reticulated with yellow and red, more or less purplish.

Habitat.—Small and immature individuals are found in the Beaufort, N.C., harbor region; larger individuals occur in deep water off the coast; between tides among rocks to 435 fathoms.

Type localities.—Nova Scotia to Cape Cod.

Known range.—Nova Scotia to south of Tortugas, Fla.; Bermuda.

Remarks.—This species has a fossil record dating from the Miocene of North America (Mac-

Kay, 1943). Ovigerous females are recorded in June from southern Florida.

Family Xanthidae

Crabs with body transversely oval or transversely hexagonal. Front broad, never produced in form of a rostrum. Last pair of legs normal. Antennules folding obliquely or transversely. Male openings rarely sternal (Rathbun, 1930a).

In the key to the genera of Xanthidae in the Carolinas it has been impossible to use characters which show the general relationships unless pleopods of the males are employed. Differences between genera are often subtle and the general worker is, therefore, compelled to use a combination of trivial characters for identification. Because most of the genera occurring in the Carolinas contain a single species, the generic key is in large part also a key to species. Parts of the key have been adapted from Rathbun (1930a) and Ryan (1956).

Arrangement of the genera differs in some respects from that of Rathbun and is based on similarities and differences in the first pair of male pleopods. In such arrangement I follow broadly the arrangements of Stephensen (1945) and Monod (1956). As in Rathbun (1930a) and Monod (1956), no attempt is made to divide the family Xanthidae into subfamilies, though at least three well-marked groups appear in the Carolinas, and perhaps the third of these groups (fig. 183) could be split into additional groups.

KEY TO GENERA IN THE CAROLINAS

- a. Entire body and legs with surface deeply and intricately eroded, resembling piece of stony coral. *Glyptoxanthus* (p. 185).
- aa. Entire body and legs with surface not deeply and intricately eroded.
 - b. Antennae widely separated from orbits..... *Eriphia* (p. 182).
 - bb. Antennae not separated from orbits.
 - c. Chelipeds with a large notch clearly forming an open hole between carpus and hand when viewed frontally with chelipeds fully pressed against body..... *Carpoporos* (p. 186).
 - cc. Chelipeds without a large notch clearly forming an open hole between carpus and hand when viewed frontally with chelipeds fully pressed against body.
 - d. Extreme edge of frontal margin with shallow transverse groove, each half appearing double (under magnification).
 - e. Carapace more or less nodose in front, upper edge of frontal groove formed by line of nodules. *Leptodius* (p. 192).
 - ee. Carapace not nodose in front but with transverse ridges on dorsum..... *Rhithropanopeus* (p. 187).
 - dd. Extreme edge of frontal margin not transversely grooved, each half presenting but a single edge (under magnification).
 - e. Teeth of anterolateral border subtriangular or with edges flattened and rounded; carapace never nodose.
 - f. Carapace with regions on dorsum defined; carapace not smooth to unaided eye.
 - g. Major cheliped with a more or less conspicuous tooth at base of dactyl, tooth larger than adjacent teeth and often of contrasting color.

- h. Third and fourth teeth of anterolateral border definitely pointed forward with outer borders curved.
 - i. Tooth at base of major dactyl large and conspicuous; body definitely arched above. *Panopeus* (p. 196).
 - ii. Tooth at base of major dactyl present but often not large and conspicuous; posterior two-thirds of carapace flattened above. *Eurypanopeus* (p. 194).
- hh. Third and fourth teeth of anterolateral border triangular and pointing outward or slightly forward, outer borders not conspicuously curved. *Hexapanopeus* (p. 188).
- gg. Major cheliped with no tooth at base of dactyl, or with obsolescent tooth little if any larger than adjacent teeth.
 - h. A red spot on internal face of ischium of third maxillipeds. *Eurypanopeus* (p. 194).
 - hh. No red spot on internal face of ischium of third maxillipeds. *Neopanope* (p. 190).
- ff. Carapace with regions on dorsum obsolete; carapace smooth to unaided eye.
 - g. Fingers white; anterolateral teeth pointed or rounded. *Eurytium* (p. 199).
 - gg. Fingers black; anterolateral teeth broad, not pointed, with occasional exception of most lateral tooth; often attains large size. *Menippe* (p. 183).
- ee. Teeth of anterolateral border usually distinctly spiny or spiniform; sometimes subtriangular, serrated or with spiny tips, and with carapace more or less nodose (nodes occasionally small).
- f. Carapace nearly devoid of hairs and with nodose areas on front and anterolateral portions usually clearly evident, though sometimes poorly developed; adult size small. *Micropanope* (p. 192).
- ff. Carapace with either long, plumose hairs, numerous short hairs, or both.
 - g. Carapace and chelipeds variably spiny; not nodose; with long plumose (clubbed) hairs, short hairs, or both. *Pilumnus* (p. 177).
 - gg. Carapace with patches of nodules on anterolateral margins extending back from front; with close pile of short hair only; body massive, thick. *Lobopilumnus* (p. 181).

Genus *Pilumnus* Leach, 1815

Rathbun, 1930a, p. 481.—Hemming, 1958b, p. 35.

KEY TO SPECIES IN THE CAROLINAS

- a. Hair not covering whole carapace or not forming so thick a coat as to conceal surface beneath.
 - b. Two or more superhepatic spines. *sayi* (p. 177).
 - bb. No superhepatic spines. *dasyopodus* (p. 178).
- aa. Hair covering whole carapace and forming a thick coat concealing surface beneath (hair sometimes worn off).
 - b. Chelipeds spinose above; a transverse row of long hairs across front. *floridanus* (p. 179).
 - bb. Chelipeds not spinose above; carapace tuberculate, but tubercles often sparse and low.
 - c. Tubercles of carapace not numerous nor prominent, upper margin of orbit not spinose. *lacteus* (p. 180).
 - cc. Tubercles on anterior half of carapace and upper surface of chelipeds numerous, upper margin of orbit with truncate spines (but occasionally these poorly developed). *pannosus* (p. 181).

Pilumnus sayi Rathbun. Hairy crab

Figures 157 A, B; 158

Cancer aculeatus Say, 1818, p. 449.

Pilumnus sayi Rathbun: 1897b, p. 15.—Hay and Shore, 1918, p. 440, pl. 35, fig. 4.—Rathbun, 1930a, p. 484, pl. 200, figs. 1-2; pl. 201, figs. 4-7 (rev.).

Recognition characters.—Carapace about three-fourths as long as wide, anterior half semicircular, strongly deflexed, sparsely covered with long filiform and plumose hairs. Anterolateral border with four marginal spines including outer

orbital; two curved spines on hepatic region with sometimes one, two, or three supplementary spines; one long spine and sometimes spiniform tubercles between first and second marginal spines below margin. Orbit armed with three long spines above, and four long and two to four short spines below. Front advanced, deeply notched in center, less so on each side, armed with about four spines on each side.

Superior surfaces of chelipeds and walking legs with many filiform and plumose hairs; carpal and propodal articles most thickly covered and with several strong spines as well. Chelipeds large, unequal; carpus with 15 or 20 erect dark spines; spines of hand strong and acute above but becoming smaller on external surface, spines tending to arrangement in rows on large hand; fingers ribbed, dark, and with obtuse teeth; dactyl spiny above at base.

Measurements.—Carapace: male, length, 23 mm.; width, 32 mm.

Variations.—The specimen taken on Frying Pan Shoal off North Carolina (Charleston Museum No. 38.228) reported by Lunz (1939) appears to be an aberrant specimen of *Pilumnus sayi* rather than *P. marshi*. The specimen lacks superhepatic spines on the carapace but otherwise more nearly resembles *P. sayi* than any other Western Atlantic species of *Pilumnus*.

Color.—Grayish brown irregularly suffused with red or purple on body and legs; spines black, horn color, or purple; fingers of chelae black or brownish purple.

Habitat.—This species is fairly common in the Carolinas, and is often taken on shelly bottom. It has been taken from wharf piles, buoys (Lunz, 1937a), the sponge *Stematomenia strobilina* (Lamarck) (Pearse, 1934), and from offshore reefs (Pearse and Williams, 1951). From low-water mark to 49 fathoms.

Type locality.—Georgia and east Florida.

Known range.—North Carolina through Gulf of Mexico and West Indies to Curaçao.

Remarks.—Ovigerous females occur in the Carolinas from May to August, and as early as March in Florida (Wass, 1955). Chamberlain (1961) reported four zoeal stages and one megalops stage in the larval development of the species,

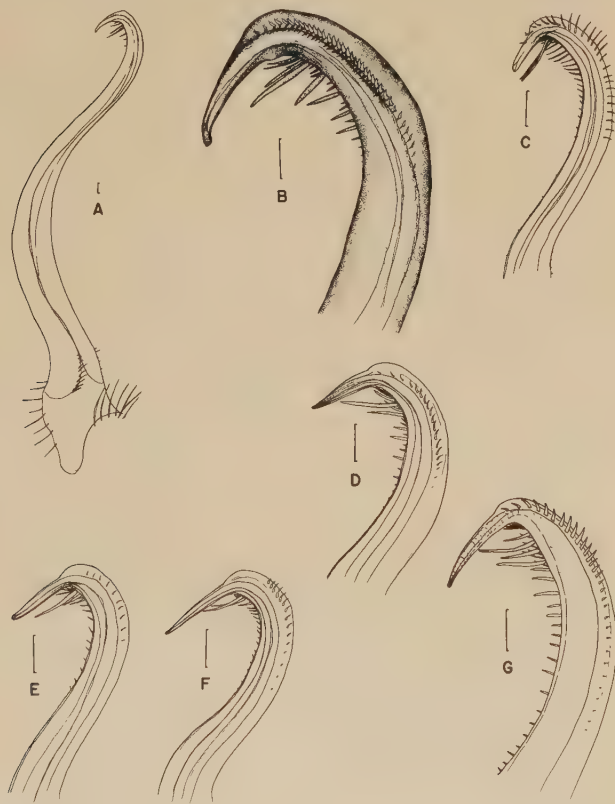


FIGURE 157.—Male first pleopods in medial view; A, *Pilumnus sayi* Rathbun, entire pleopod; B, *Pilumnus sayi* Rathbun, tip in detail; C, *Pilumnus dasypodus* Kingsley, tip; D, *Pilumnus floridanus* Stimpson, tip; E, *Pilumnus lacteus* Stimpson, tip; F, *Pilumnus pannosus* Rathbun, tip; G, *Lobopilumnus agassizii* (Stimpson), tip; 0.125 mm. indicated.



FIGURE 158.—*Pilumnus sayi* Rathbun. A, male in dorsal view, walking legs of left side not shown, 10 mm. indicated; B, large chela in frontal view, 10 mm. indicated.

but did not describe the stages in detail. He found that larval development time varied with temperature (18 days at 30° C., 28 at 21° C.) and with food. Larvae matured most rapidly when fed *Artemia salina* nauplii, did moderately well on *Artemia* and algae, but did not transform at all when fed algae alone.

Pilumnus dasypodus Kingsley

Figures 157C, 159

Pilumnus dasypodus Kingsley, 1879, p. 155.—Rathbun, 1930a, p. 493, pl. 200, figs. 5–6 (rev.).

Recognition characters.—Carapace thinly covered on anterior two-thirds with long, fine hair and occasional stouter setae; upper surface of chelipeds and walking legs similarly clothed; small sharp granules on anterolateral region. Anterolateral border with four spines including small outer orbital; spines with bases conical, extremities long, slender, incurved. Orbital border with three or four spines above and about seven below. Frontal lobes separated by a

median V- or U-shaped notch; margins furnished with short spines or sharp granules, with an outer tooth separated from remainder of margin by a U-shaped notch.

Chelipeds unequal, spinose, and granulate except for smooth and naked lower distal two-thirds of outer surface of major palm, spines and granules not arranged in rows on upper part of major palm; fingers of minor chela grooved on outside, dactyls with rows of sharp granules and hairs at base. Walking legs spinose above.

Measurements.—Carapace: male, length, 11 mm.; width, 15 mm.

Color.—Body and claws brownish-red color, legs much lighter; fingers and extremities of spines brown (Milne Edwards in Rathbun, 1930a).

Habitat.—This species has been taken from pilings, jetties, and buoys (Lunz, 1937a), and from offshore reefs (Pearse and Williams, 1951) in the Carolinas; and from similar situations elsewhere (Rathbun, 1930a) including loggerhead sponge *Speciospongia vespara* (Lamarck) (Pearse, 1934). One-half to 16 fathoms.

Type locality.—Key West, Fla.

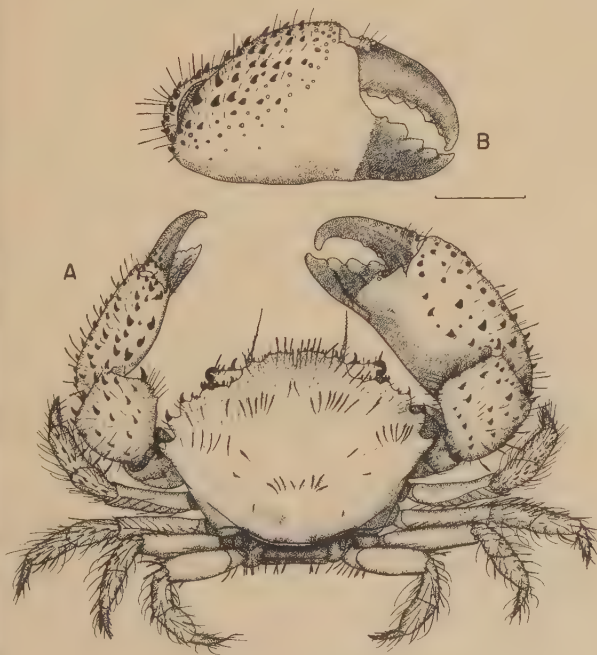


FIGURE 159.—*Pilumnus dasypodus* Kingsley. A, male in dorsal view; B, large chela in frontal view; 5 mm. indicated.

Known range.—Off Cape Hatteras, N.C., through Gulf of Mexico and West Indies to State of Santa Catarina, Brazil.

Remarks.—This species is not so common in the Carolinas as *P. sayi*, and small specimens of *dasypodus* are not always easily distinguished from *sayi*. Rathbun (1930a) stated that, "*dasypodus* is less heavily clothed with hair than *sayi* and less ragged looking. The front is more deflexed and less advanced, therefore appears wider. The spines and tubercles of the major palm in *sayi* are arranged more or less in rows and these rows have a tendency to encroach on the lower distal half; in *dasypodus* there are seldom any definite rows and the lower distal two-thirds or one-half in both sexes is smooth and bare. The immovable finger of the major chela in *dasypodus* is a little longer than in *sayi*."

Lunz (1937a) reported ovigerous females from April through August in the Carolinas, and they have been found in North Carolina in September. In the West Indies they occur at all seasons of the year (U.S. National Museum records).

Pilumnus floridanus Stimpson

Figures 157D, 160

Pilumnus floridanus Stimpson, 1871a, p. 141.—Rathbun, 1930a, p. 507, pl. 205, figs. 3-4 (rev.).

Recognition characters.—Carapace covered with dense, short pubescence thinning behind, and with a few longer clavate hairs, a conspicuous transverse series of these crossing frontal region. Anterolateral margin with four somewhat conical spines; a small subhepatic spine between outer orbital and second spine; hepatic region slightly roughened but with no spines. Frontal lobes almost bare, edge slightly oblique, entire, with median triangular notch and rounded lateral notches; tooth at outer angle minute, deflexed. Orbital margin unarmed above, with 8 to 10 spinules below.

Chelipeds spinose above; merus with two spines near distal end on upper surface; carpus armed over entire exposed surface; spines on hand becoming pointed tubercles on outer surface. Male with large hand smooth and bare on outer lower half or less of surface, smooth portion more restricted in female. Walking legs spined above.

Measurements.—A small species. Carapace: male, length, 7 mm.; width, 10 mm.

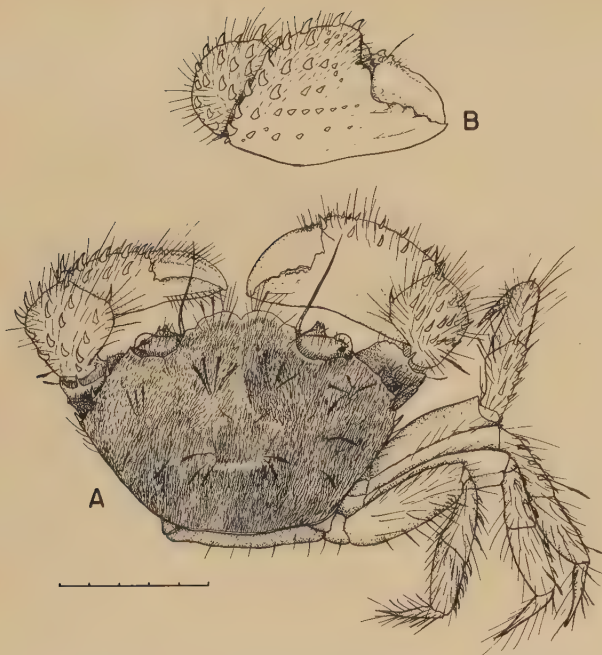


FIGURE 160.—*Pilumnus floridanus* Stimpson. A, animal in dorsal view, walking legs of left side not shown; B, large chela in frontal view; 5 mm. indicated.

Habitat.—In North Carolina this species has been taken from an offshore reef (Pearse and Williams, 1951) and has been found in sponges. Rathbun (1930a) listed it as taken from rocks, grass, and a variety of bottoms. Low-tide mark to about 80 fathoms.

Type locality.—Tortugas, [Fla.].

Known range.—Off Cape Lookout, N.C., through eastern Gulf of Mexico, and Yucatan Channel, to Honduras; through West Indies to Venezuela.

Remarks.—This species is not common north of Florida. Ovigerous females are known from March to August in Florida (Rathbun, 1930a, in part) and they have been taken in February in North Carolina.

***Pilumnus lacteus* Stimpson.** Small hairy crab

Figures 157E, 161

Pilumnus lacteus Stimpson, 1871a, p. 142.—Hay and Shore, 1918, p. 440, pl. 35, fig. 3.—Rathbun, 1930a, p. 511, pl. 205, figs. 1-2 (rev.).

Recognition characters.—Carapace about three-fourths as long as wide, covered with short velvet-like pubescence easily rubbed off (and often is), nearly smooth, sparse tubercles almost invisible

through hairy coating; a row of five tubercles paralleling anterolateral and orbital margins, others scattered. Anterolateral margins with four anteriorly directed teeth, first or outer orbital small. Front depressed, deeply notched in middle, and with a smaller notch near eye. Orbital margin occasionally a bit uneven but not tuberculate.

Chelipeds dissimilar in size but otherwise nearly alike, stout, setose, and plumose-hairy, somewhat tuberculate above, but naked and polished below and on ventral half or two-thirds of both inner and outer surfaces of chelae; merus with two similar curved spines on upper margin distally; carpus with a stout spine on inner angle.

Measurements.—Carapace: male, length, 12 mm.; width, 15 mm.

Color.—Gray or pinkish, with plumose hairs whitish or cream colored; hands and tips of legs light red.

Habitat.—This crab may be found by a careful search of wharf pilings about the Beaufort, N.C., harbor area, but is rarely taken in dredge hauls. It has been taken from buoys both in sounds and at sea in South Carolina (Lunz, 1937a). Rathbun (1930a) reported it from a variety of situations farther south. Near low-tide mark to about 8 fathoms.

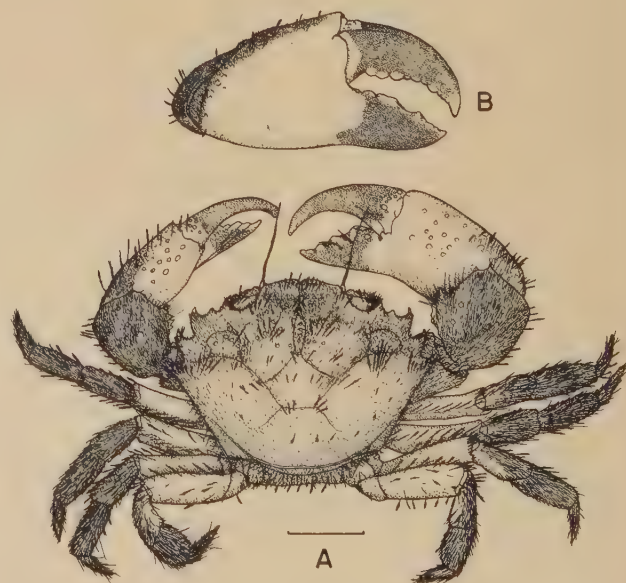


FIGURE 161.—*Pilumnus lacteus* Stimpson. A, animal in dorsal view; B, large chela in frontal view; 5 mm. indicated.

Type locality.—Cruz del Padre, Cuba, and Key West, Fla.

Known range.—Near Beaufort, N.C., to Florida; Cuba.

Remarks.—Ovigerous females have been reported in December from Florida, and in May from Cuba (Rathbun, 1930a) and South Carolina (Lunz, 1937a).

Pilumnus pannosus Rathbun

Figures 157F, 162

Pilumnus pannosus Rathbun, 1896b, p. 142.—Rathbun, 1930a, p. 514, figs. 4-5 (rev.).

Recognition characters.—Carapace about three-fourths as long as wide, almost entirely covered with unevenly distributed, soft, thick, velvety pubescence, with scattered longer club-shaped setae giving ragged appearance; lobulations of anterior portion of carapace and tubercles of chelipeds showing through pubescence. Anterior half of carapace and upper surface of chelipeds and legs dotted with beadlike tubercles. Anterolateral margin with four triangular spines (outer orbital small) having slender forward-projecting tips; subhepatic spine between first and second tooth well developed. Frontal lobes (when well formed) broadly subtriangular, granulate on margin, separated by a V-shaped notch; outer tooth of front almost triangular, acute (blunt at tip in some specimens). Upper margin of orbit with three truncate teeth covered by pubescence, lower margin with a row of short, stout, truncate teeth or tubercles.

Chelipeds with upper surface tuberculate but usually with large part of outer surface smooth and naked; small hand with outer surface often rough with rows of spines; dactyls with a few tubercles near articulation. Male with shallow grooves on fingers, female with well-defined grooves on minor fingers and fixed major finger. Walking legs pubescent, fringed with club-shaped setae mixed with long fine hair.

Measurements.—Carapace: male, length, 9 mm.; width, 12 mm.

Color.—Carapace under pubescence and bare part of palms bright red (Milne Edwards in Rathbun, 1930a).

Habitat.—Pearse and Williams (1951) listed this species as taken from a submerged rocky reef, and Rathbun (1930a) listed it from similar situa-

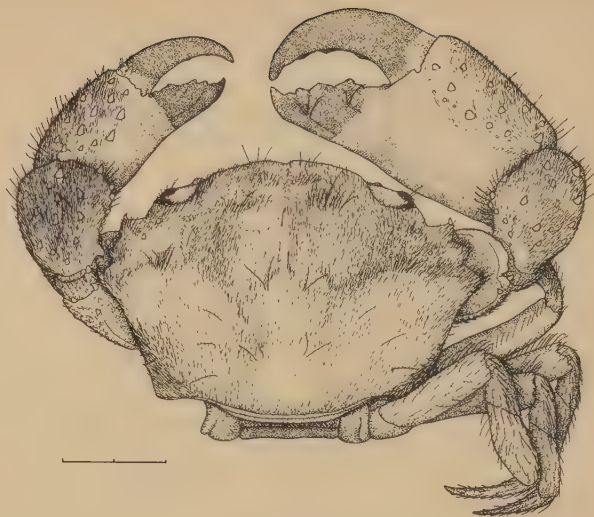


FIGURE 162.—*Pilumnus pannosus* Rathbun. Male in dorsal view, walking legs of left side not shown, 2 mm. indicated.

tions, as well as from sponges and corals. A few feet to 9 fathoms.

Type locality.—Key West, Fla.

Known range.—Bogue Sound off Beaufort, N.C., to Port Aransas, Tex.; West Indies to Virgin Islands.

Remarks.—The species has rarely been taken north of Florida. Rathbun (1930a) listed ovigerous females in December and January from Florida, and they are known from April to August between South Carolina and Cuba.

Genus *Lobopilumnus* Milne Edwards, 1880

Rathbun, 1930a, p. 525.

Lobopilumnus agassizii (Stimpson)

Figures 157G, 163

Pilumnus agassizii Stimpson, 1871a, p. 142.

Lobopilumnus agassizii: Hay and Shore, 1918, p. 441, pl. 34, fig. 5.—Rathbun, 1930a, p. 526, pl. 211 (rev.).

Recognition characters.—Regions of carapace protuberant, surface pubescent, except naked and thickly granulated on anterior and anterolateral regions; depressions between regions broad, occupying as much area as regions themselves. Front consisting of two large lobate masses deeply separated from each other and from orbits. Orbital region protuberant and granulate, margin crenulated with granules, with two fissures above and two very narrow ones below. Anterolateral margin with three triangular, spine-tipped teeth of moderate, equal size; subhepatic tooth distinct.

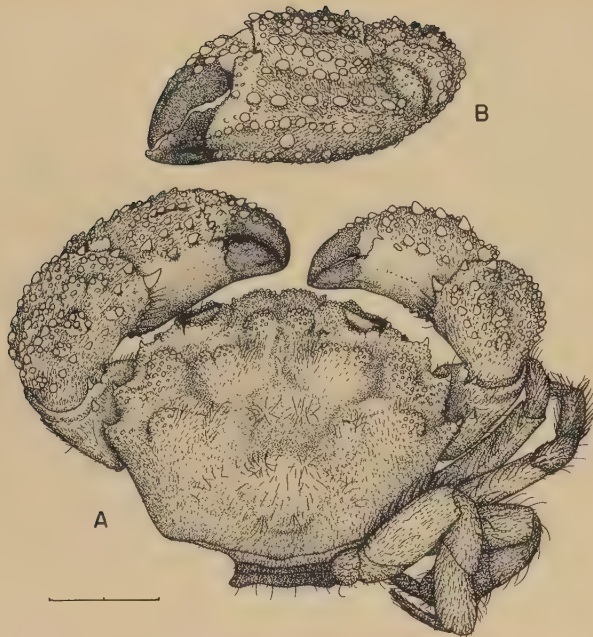


FIGURE 163.—*Lobopilumnus agassizii* (Stimpson). A, male in dorsal view, walking legs of left side not shown; B, large chela in frontal view, 10 mm. indicated.

Chelipeds short, stout; carpus with forwardly directed granules, confluent exteriorly; hands with superior and outer surfaces covered with small prominent mammillary tubercles, arranged largely in rows on outer surfaces and having apices directed forward. Walking legs pubescent and hairy, carpal and propodal articles with minute spines above.

Measurements.—Carapace: female from North Carolina, length, 16 mm.; width, 21 mm.

Variations.—Rathbun (1930a) stated that this species is variable as to the number and prominence of regions on the carapace, and she recognized four environmental forms within the species. Because only one specimen has ever been reported from North Carolina, and this is no longer extant, it is not possible to assign a form or forms to this area.

Color.—Gray above with granules and knobs yellowish red and reddish brown; legs white or with whitish spots (Schmitt in Rathbun, 1930a).

Habitat.—In Bermuda, Verrill (1908) found the carapace and legs of this species often thickly covered, sometimes almost concealed, by a coating of calcareous mud and sand adhering to hairs on

the back. He found it most frequently under stones and dead corals at low tide. Pearse (1934) reported this crab from loggerhead sponge *Speciospongia vespara* (Lamarck). Low-tide mark to 28 fathoms.

Type locality.—Typical form: East and Middle Keys, Tortugas, Fla.

Known range.—North Carolina; southern and west Florida; Yucatan; Cuba; Trinidad; Bermuda.

Remarks.—Ovigerous females are known from February to July in Florida and Cuba (Rathbun, 1930a, in part).

Genus *Eriphia* Latreille, 1817

Rathbun, 1930a, p. 545.

Eriphia gonagra (Fabricius)

Figures 164 A, B, C; 165

Cancer gonagra Fabricius, 1781, p. 505.

Eriphia gonagra: Hay and Shore, 1918, p. 439, pl. 35, fig. 6.—Rathbun, 1930a, p. 545, text-fig. 83, pl. 222 (rev.).

Recognition characters.—Carapace approximately quadrate, about one-fourth wider than long, flattened, with regions clearly marked off on anterior two-thirds; surface nearly smooth posteriorly but granulate anteriorly, and with two transverse lines of subspinous granules, one in front of epigastric lobes and another across protogastric and hepatic lobes. Front wide, strongly deflexed, and divided into four lobes, both median lobes broader and more advanced than lateral ones, and with a finely granulate border. Lateral lobes forming front of raised margin of orbits and in contact beneath with a prolongation of infraorbital plate, thus completely excluding antenna from orbit. Anterolateral margins each with a row of five spines including outer orbital, behind and inside these a few squamiform tubercles.

Chelipeds unequal, strong, swollen; hands covered with large, round, flattened, squamiform tubercles, more elevated on small than on large hand; carpus with less prominent tubercles; dactyls with squamiform tubercles above at base; major dactyl with large rounded tooth at base. Walking legs rather slender, their distal three articles with fine stiff hairs.

Measurements.—Carapace: male, length, 31 mm.; width, 44 mm.

Color.—Gaily colored. Anterior half of carapace and a broad median stripe extending to posterior margin, dark purplish brown, legs a lighter tint of same color; front margined with brownish orange. Sides of carapace, upper surface of chelipeds, dactyls, bases of legs, and a narrow band on distal margin of other articles, light yellow. Tubercles on upper half of chelipeds, dark blue; on lower half, yellow. Underparts of body and chelipeds, white, fingers brown. Rathbun (1930a) gives another detailed color description.

Habitat.—The species has been found in a variety of situations: under flat rocks above the watermark, in seaweed, sponges, brackish ponds,



FIGURE 165.—*Eriphia gonagra* (Fabricius). Male in dorsal view, walking legs of left side not shown, 10 mm. indicated.

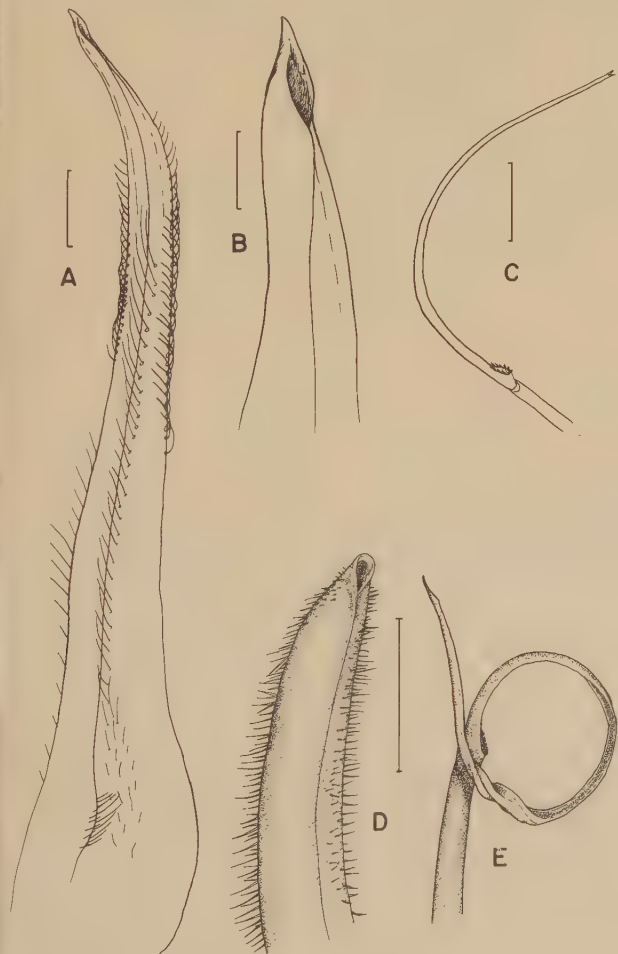


FIGURE 164.—*Eriphia gonagra* (Fabricius) ; A, entire first pleopod, 0.75 mm. indicated ; B, tip of first pleopod, 0.25 mm. indicated ; C, tip of second pleopod, 0.75 mm. indicated ; *Menippe mercenaria* (Say) ; D, tip of first pleopod ; E, tip of second pleopod ; 5 mm. indicated.

tide pools, and on coral reefs. Shoreline to shallow water of uncertain limits.

Type locality.—Jamaica.

Known range.—North Carolina to Argentine Patagonia.

Remarks.—Ovigerous females are known from March to September in various parts of the West Indies and southern Florida; in October from Santa Catarina, and February from Bahia, Brazil (Rathbun, 1930a, in part).

Genus *Menippe* de Haan, 1833

Rathbun, 1930a, p. 472.

***Menippe mercenaria* (Say).** Stone crab

Figures 164 D, E; 166

Cancer mercenaria Say, 1818, p. 448.

Menippe mercenaria: Hay and Shore, 1918, p. 439, pl. 35, fig. 8.—Rathbun, 1930a, p. 472, text-fig. 78, pls. 191-193 (rev.).

Recognition characters.—Carapace transversely oval, approximately two-thirds as long as wide, convex, nearly smooth to unaided eye, minutely granulate and punctate. Anterolateral border divided into four lobes: first two wide, third wide but dentiform, fourth much narrower and dentiform. Front with a median notch and a broad trilobulate lobe on each side. Orbital border thick, fissures indistinct.

Chelipeds large and heavy, unequal, nearly smooth; inside surface of hands with a patch of fine, oblique, parallel striae serving as a stridulating organ and adapted for playing against thick edge of second and third anterolateral teeth and



FIGURE 166.—*Menippe mercenaria* (Say). Male in dorsal view, approximately $\times 0.6$ (after Rathbun, 1884).

outer suborbital tooth; dactyl of major chela with a large basal tooth, and immovable finger with a large subbasal tooth; fingers of minor chela with numerous small teeth. Walking legs stout, hairy distally.

Measurements.—Female: length of carapace, 79 mm., width, 116 mm.; length of cheliped, 155 mm. This is the largest xanthid species in the area.

Color.—Young individuals dark purplish blue, very young always with a white spot on carpus. Older individuals become a dark brownish red more or less mottled and spotted with dusky gray; fingers dark.

Habitat.—The young resort to deeper channels of saltier estuaries where they live under shell

fragments. Young have also been taken from buoys in South Carolina (Lunz, 1937a). On attaining a width of about one-half inch, they apparently move to shallower water and may be found among oyster shells, on rocks, pilings, and about jetties. (In northwest Florida, *M. mercenaria* apparently prefers turtle grass (*Thalassia testudinum*) flats (Wass, 1955).) Here they live until they have attained nearly full size when they may move to some shoal and make burrows just below low-tide mark. Such burrows are about 6 inches in diameter and extend for 12 to 20 inches. The crabs can be taken from burrows by hand if the collector keeps his hand against the upper wall of the hole, and a number of specimens for

the Institute of Fisheries Research Laboratory have been taken in this manner. Specimens have also been taken from baited plots set for capture of blue crabs, and in trawls from the oceanic littoral. Surface to 28 fathoms.

Type locality.—"The Southern States."

Known range.—Cape Lookout, N.C., to Yucatan, Mexico; Bahamas; Cuba; Jamaica.

Remarks.—The genus *Menippe* has a fossil record in North America dating from the Cretaceous, the thick, hard exoskeleton no doubt enhancing its chances of fossilization. The record for *M. mercenaria* dates from the Pleistocene (Rathbun, 1935).

Ovigerous females have been taken from May to July (perhaps August) in North Carolina. Binford (1912) discussed spermatogenesis and fertilization in the species and gave notes on spawning habits. Porter (1960) reviewed literature on fecundity and larval development of *M. mercenaria* and described zoeal stages reared in the laboratory. Females have been observed to molt, then mate immediately after spawning in the laboratory, and produce a new sponge a week after the previous egg mass has hatched. Subsequent to such mating, more than one mass of eggs may be produced before another molt or mating occurs. Females have been known to produce six egg masses in 69 days, each mass containing between 500,000 and 1 million viable eggs.

Porter described one prezoal and six zoeal stages for larvae reared in culture on *Artemia* nauplii, but the prezoal and sixth stages were considered as probably atypical. Length of larval life was approximately 27 days under the conditions imposed, and from experimental data it was concluded that warm water of high salinity is needed for optimum survival.

Manning (1961) gave data on relative growth, showing that the juveniles have a relatively broader front than adults. Both he and Wass (1955) pointed out the superficial resemblance of young *M. mercenaria* to *Panopeus herbstii* and *Eurytium limosum*, and Manning gave distinguishing characters for each species at comparable sizes. Further, the stridulating mechanism was shown not to be visible in small specimens and, indeed, stridulation itself has not been ob-

served in the adults (Guinot-Dumortier and Dumortier, 1960).

In studies on the relationship of number and volume of gills to oxygen consumption, Pearse (1929) and Ayers (1938) found this form, along with other mud crabs, intermediate between the sluggish common spider crab and the more active, partially terrestrial, fiddler and ghost crabs. Pearse also found that *M. mercenaria* could withstand considerable dilution of the environment with fresh water. Gray (1957) found gill area per gram of weight to be intermediate in an array of species ranging from land to shallow-water habitats.

Menzel and Hopkins (1956) found the stone crab in Louisiana to be an active predator on oysters. The powerful crabs killed small and large oysters alike. Though predation was found to be lowest in winter and highest in fall, the average rate of consumption in the area studied was 219 oysters per crab per year (=1,000 bushels of oysters per acre if this number were available).

Genus *Glyptoxanthus* Milne Edwards, 1879

Rathbun, 1930a, p. 263.

Glyptoxanthus erosus (Stimpson)

Figures 167, 183A

Actaea erosa Stimpson, 1859, p. 51.

Glyptoxanthus erosus: Rathbun, 1930a, p. 263, pl. 107 (rev.).



FIGURE 167.—*Glyptoxanthus erosus* (Stimpson). Animal in dorsal view, detail shown on right side, 5 mm. indicated.

Recognition characters.—Surface of body and legs covered with rough vermiculations, with furrows or cavities between them narrow, making a regular pattern and giving body an eroded appearance; elevated portions between furrows or cavities formed by masses of small granules crowded together producing rough surface in young and half-grown individuals, but variably worn smooth in old ones; margins of cavities with short pubescence. Carapace areolated, but divisions obscured to large extent by character of surface; lateral boundaries of gastric region and median suture from front to middle of gastric region deep. Front steeply inclined, median lobes evenly rounded, margins granulate. Ischium of third maxilliped with deep, longitudinal, central groove.

Chelae short and broad, upper surface divided by furrows into transverse tuberculate ridges, outer surface divided into longitudinal tuberculate ridges; fingers short, deeply grooved, even toothed; dactyls tuberculate at base on upper side. Walking legs with hairy edges, dactyls pubescent.

Measurements.—Carapace: male, length, 39 mm.; width, 54 mm.

Color.—Rathbun (1930a) described a specimen in formalin as cream white with blotches and small spots of bright red, color especially persistent on walking legs, with dactyls red at base and yellowish distally.

Habitat.—The species has been taken from rocks and the alga *Halimeda* in shallow water, from coarse sand, and from sponges and coral reefs in deeper water. Low-tide mark to 37 fathoms.

Type locality.—Florida.

Known range.—Cape Lookout, N.C., to Yucatan; through West Indies to Guadeloupe.

Remarks.—Ovigerous females have been taken off northeast Florida in January.

Genus *Carpoporus* Stimpson, 1871

Rathbun, 1930a, p. 269.—Hemming, 1958b, p. 14.

Carpoporus papulosus Stimpson

Figure 168, 183B

Carpoporus papulosus Stimpson, 1871a, p. 139.—Rathbun, 1930a, p. 269, pl. 110, figs. 3–6, pl. 111 (rev.).

Recognition characters.—Carapace subhexagonal, nearly as long as broad, naked above; regions



FIGURE 168.—*Carpoporus papulosus* Stimpson. A, animal in dorsal view, legs of left side not shown; B, cheliped in frontal view partially extended; 3 mm. indicated.

protuberant, somewhat wartlike and granulated, gastric and epibranchial regions prominent. Two or three small, spiniform lateral teeth, interspaces armed with denticles. Front strongly projecting at middle, bilobed, margin concave, inner end rectangular, outer end spiniform. Peduncle of eye granulated; orbit with margin granulate above. Exposed surface of third maxilliped with beadlike granules.

Chelipeds when retracted having a large hole between carpus and hand for passage of water to afferent branchial apertures; inner surface of hand with two unequal peglike spines near middle forming a kind of filter in front of branchial opening; carpus and hand sculptured externally with granulated protuberances, arranged in four or five serial rows on hand; hand serrate above with four teeth partially joined; fingers stout, short. Walking legs hairy below.

Measurements.—Carapace: male, length, 13 mm.; width, 16 mm.

Habitat.—Eighteen to 62 fathoms.

Type localities.—Southwest of Tortugas, and off Carysfort Reef, [Fla.].

Known range.—Between Capes Hatteras and Lookout, N.C.; Cape Catoche, Yucatan, Mexico.

Genus *Rhithropanopeus* Rathbun, 1898

Rathbun, 1930a, p. 455.—Hemming, 1958b, p. 37.

Rhithropanopeus harrisi (Gould)

Figures 169, 183C

Pilumnus harrisi Gould, 1841, p. 326.

Rhithropanopeus harrisi: Hay and Shore, 1918, p. 441, pl. 35, fig. 5.—Rathbun, 1930a, p. 456, pl. 183, figs. 7–8 (rev.).

Recognition characters.—Carapace subquadrate, approximately three-fourths as long as wide, much less convex from side to side than from front to back, sparsely pubescent toward anterolateral angles; protogastric regions with two transverse lines of granules; a similar line from one posterior lateral tooth to opposite one across mesogastric region. Front almost straight, slightly notched, and with margin transversely grooved, appearing double when viewed from in front. Postorbital angle and first anterolateral tooth completely coalesced; first and second developed anterolateral teeth of about same size and perhaps larger than last one.

Chelipeds unequal and dissimilar; carpus not grooved above and with a moderately developed internal tooth; chelae indistinctly costate above. Major chela with short immovable finger and strongly curved dactyl. Minor chela with proportionately longer immovable finger and long straight dactyl. Walking legs long, slender, compressed, and somewhat hairy.

Measurements.—Carapace: male, length, 15 mm.; width, 19 mm.

Variations.—The chelipeds are nearly smooth in old individuals, but in small specimens the carpus is rough with lines and bunches of granules, the distal groove deep, the upper margin of palm with two granulate ridges, and the upper edge of the fingers granulate.

Color.—Brownish above, paler below; fingers light.

Habitat.—In Chesapeake Bay, Ryan (1956) found this species distributed primarily in the upper bay and in tributaries of the lower bay in depths of 0 to 5 fathoms. A similar distribution has been found for upper Delaware Bay (McDermott and Flower, 1953) and the tributaries of the Neuse River estuary in North Carolina. Ryan collected specimens in waters ranging from fresh to 18.6‰. The places from which the form was taken always afforded some kind of shelter—oyster bars, living and decaying



FIGURE 169.—*Rhithropanopeus harrisi* (Gould). Frontal aspect of body viewed from above, 3 mm. indicated.

vegetation, old cans, and other debris. Bousfield (1955) found larvae of the species in water from 4 to no higher than 28.5 ‰ salinity. Surface to 20 fathoms.

Type locality.—Cambridge Marshes and Charles River, Mass.

Known range.—The original range of this species was in fresh to estuarine waters from New Brunswick, Canada, to Veracruz, Mexico; north-east Brazil. The species has been introduced on the west coast of the United States and in parts of Europe.

Remarks.—Connolly (1925) stated that four zoeal stages and one megalops stage comprise the larval and postlarval development of this species. These conclusions were based on study of plankton taken from the Miramichi River estuary, New Brunswick, Canada, in August. Chamberlain (1962) confirmed and supplemented Connolly's account with eggs taken from Chesapeake Bay and cultured in the laboratory. Duration of larval stages was twice as long when zoeae were fed copepod nauplii and algae as when fed nauplii alone. In an array of salinities and temperatures, development was found to proceed best at 6 to 10 ‰ salinity. Developmental time increased with decreasing temperature. Developmental times of larvae in nature were found to be in agreement with results of laboratory culturing at similar salinities and temperatures. Mortality rates for larvae in nature were found to be lower than expected. A relatively high rate was postulated for the megalops or early crab stages. Presence of adult crabs in fresh water was deemed a result of migration after larval stages are complete. Hood

(1962) also described a series of larval and post-larval stages from eggs hatched and reared under laboratory conditions in Mississippi.

Ryan (1956) summarized life history data for *R. harrisii* in the Chesapeake Bay area. Ovigerous females were collected from June to September (also in April in Louisiana and Brazil). Though juveniles were found in all months of the year, they occurred most frequently in samples taken from July to October. Immature forms of undetermined sex ranged from 2.2 to 2.6 mm. in width. Immature males ranged from 3.2 to 5.0 mm. and similar females from 3.3 to 5.7 mm. in width. Ryan considered maturity to be reached the following summer at a carapace width of 4.5 mm. for males and 4.4 to 5.5 mm. in females.

Adults continue to grow and molt after maturity is reached, and males finally attain a larger size than females (up to 14.6 and 12.6 mm. wide respectively). No concrete data on number of instars throughout life are available but it is estimated that there may be four instars between attainment of the 5 and 10 mm. carapace widths.

This species has been transported from its original range to two widely separated areas of the earth. One of these is the west coast of the United States where it was reported in the San Francisco Bay area by Jones (1940) and Filice (1958), and at Coos Bay, Oreg., by Ricketts and Calvin (1952). An older and wider introduction in Europe was reviewed by Buitendijk and Holthuis (1949) who considered the European form a separate subspecies (*R. h. tridentatus* (Maitland)). Originally confined to the old Dutch Zuider Zee, the species gradually diminished in abundance there with the closing of that inland sea in 1936. In that same year it was first reported outside Netherlands waters. In 1939 it was first reported in large numbers from southern Russia in the Dnjetz and Bug River estuaries, and according to fisherman there was first observed in 1936 but certainly not present before 1932. The latest extension of range was reported by Wolff (1954) in South Harbor of Copenhagen, Denmark.

Because this form is easily collected and can tolerate a low but broad range of salinities, it has been the subject of study in investigations on the mechanism of osmoregulation (Jones, 1941; Verwey, 1957).

Genus *Hexapanopeus* Rathbun, 1898

Rathbun, 1930a, p. 383.

KEY TO SPECIES IN THE CAROLINAS

- a. Carpus slightly tuberculate.....*angustifrons* (p. 188).
- aa. Carpus tuberculate.....*paulensis* (p. 189).

Hexapanopeus angustifrons (Benedict and Rathbun).
Narrow mud crab

Figures 170, 183D

Panopeus angustifrons Benedict and Rathbun, 1891, p. 373, pl. 22, fig. 3; pl. 24, fig. 18.

Hexapanopeus angustifrons: Hay and Shore, 1918, p. 436, pl. 34, fig. 7.—Rathbun, 1930a, p. 384, pl. 169, figs. 1–2 (rev.).

Recognition characters.—Carapace hexagonal, about two-thirds to three-fourths as long as wide, convex from front to back, regions fairly well marked, surface finely granulate. Anterolateral edge thin, upturned, and divided into five teeth, first two separated by a well-defined sinus, third and fourth successively broader, fifth shorter, narrower, more distinctly directed outward; each of last two teeth with a ridge extending obliquely inward and backward for distance twice length of teeth. Front narrow, produced, divided in half by a prominent V-shaped notch; each half bilobate, with markedly sinuate anterior border forming a broad inner and small, inconspicuous outer lobe.

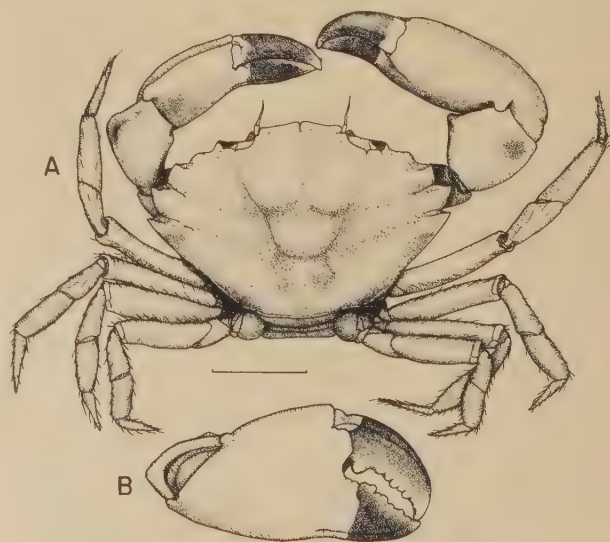


FIGURE 170.—*Hexapanopeus angustifrons* (Benedict and Rathbun). A, animal in dorsal view; B, large chela in frontal view; 5 mm. indicated.

Chelipeds strong, granulate, and finely rugose; merus with a well-developed tooth on upper margin; carpus with a moderately deep groove parallel to distal margin, an obtuse tooth at inner angle, and with superior surface rough and more or less tuberculate. Hands unequal and dissimilar; palm usually with a fairly strong ridge above and indications of one on outer surface, both ridges continued on fingers; fingers strong, slightly hooked at tips; dactyl of larger hand with strong tooth at base.

Measurements.—Carapace: length, 20 mm.; width, 28 mm.

Color.—Usually dark reddish brown or dark gray, sometimes a uniform brownish yellow or light buff; females usually darker than males and often more or less spotted; fingers black or dark brown at base, lighter at tips, color not continued on palm. Often a light yellow band along anterior border of carapace (Wass, 1955, in part).

Habitat.—Ryan (1956) found this species infrequently in the lower portion of Chesapeake Bay in from 6- to 25-fathom water (Cowles, 1930, in part) and in salinities ranging from 18 to 32‰. McDermott and Flower (1953) found the species only in the lower portion of Delaware Bay. Rathbun (1930a) recorded the species from oyster bars along the New England coast, and it is found in shelly situations in the Carolinas (Lunz, 1937a). Though it occurs in places such as Beaufort Harbor, N.C., the species is apparently not found primarily in shallow water near shore (see also Wass, 1955). Near shore to 76 fathoms.

Type locality.—Long Island Sound.

Known range.—Vineyard Sound, Mass., to Port Aransas, Tex.; Bahamas; Jamaica.

Remarks.—Ovigerous females are known from February to August in Florida, in July from North Carolina and Virginia, and in October from Texas. Ryan (1956) gave the range in carapace width of mature males as 9.7 to 28.9 mm. and of mature females as 8.4 to 20.2 mm. in Chesapeake Bay. Rathbun (1930a) considered specimens from Chesapeake Bay southward to average smaller than those from farther north.

Chamberlain (1961) reported four zoeal stages and one megalops stage in larval development of the species but did not describe the stages in detail. He found that larval development time varied with temperature (17 days at 30° C., 28 at

21° C.) and with food. Larvae matured most rapidly when fed *Artemia salina* nauplii, matured moderately well on *Artemia* and algae, but did not transform at all when fed algae alone.

Hexapanopeus paulensis Rathbun

Figures 171, 183E

Hexapanopeus paulensis Rathbun, 1930a, p. 395, pl. 170, figs. 5-6.

Recognition characters.—Carapace hexagonal, approximately two-thirds to three-fourths as long as wide, convex, regions fairly well marked, surface with approximately 12 transverse granulated lines on gastric, cardiac, and branchial regions. First tooth of anterolateral border small; second larger, broad, and shallow, with arcuate outer margin; third with nearly straight margin directed forward and inward; fourth and fifth acute and prominent; sometimes with small denticle between first, second, or third pairs of teeth. Front with edge thin, arcuate, with small, median, V-shaped notch, and each half with small lobule at outer end. Inner suborbital angle large; a raised line of granules on subhepatic region.

Chelipeds with carpus and upper part of palm roughened; carpus with approximately 15 tubercles above, an internal tooth, and below it a small tooth or denticle, distal groove deep. Hand with a superior groove and another on outer surface below upper edge, ridges bordering groove with low tubercles; fingers deeply grooved, dark or horn colored, color continued somewhat on palm, ending in an oblique line; tips light.

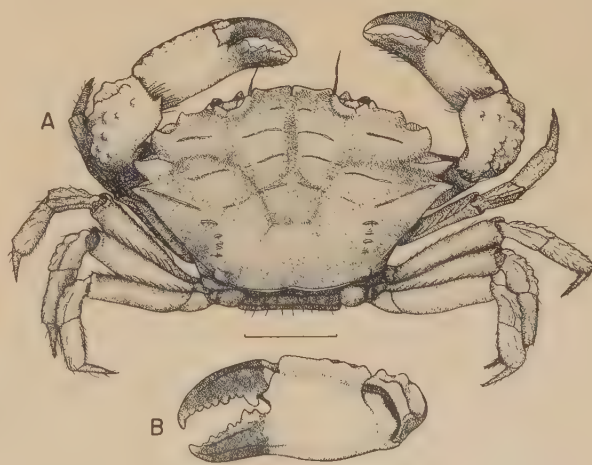


FIGURE 171.—*Hexapanopeus paulensis* Rathbun. A, animal in dorsal view; B, large chela in frontal view; 5 mm. indicated.

Measurements.—Carapace: male, length, 7 mm., width, 10 mm.; female, length, 10 mm., width, 14 mm.

Habitat.—Three fathoms (Lunz, 1937a).

Type locality.—Santos, São Paulo, Brazil.

Known range.—South Carolina, through Gulf of Mexico to State of São Paulo, Brazil.

Remarks.—This species has been reported from only a few widely separated areas. Rathbun (1930a) reported ovigerous females in September from Brazil.

Genus *Neopanope* Milne Edwards, 1880

Rathbun, 1930a, p. 366.

KEY TO SUBSPECIES IN THE CAROLINAS

- a. Fingers white or light horn colored
texana texana (p. 190).
- aa. Fingers dark colored.....*texana sayi* (p. 190).

Neopanope texana texana (Stimpson)

Figures 172, 183F

Panopeus texanus Stimpson, 1859, p. 55.

Neopanope texana texana: Rathbun, 1930a, p. 367, text-fig. 57, pl. 168, figs. 1-2 (rev.).

Recognition characters.—Carapace quite convex in both directions, high in middle, length contained in width about 1.3 times, greatest width at fifth pair of anterolateral teeth. Carapace minutely pubescent, especially in female; regions defined. First two anterolateral teeth coalesced, separated by a shallow sinus; first tooth triangular, second arcuate; third and fourth teeth sharp, with tips pointing forward; fifth tooth short, sharp, directed outward and upward; each of last two teeth with a short ridge extending inward. Front slightly produced, rounded, with small median notch.

Chelipeds smooth, unequal, and dissimilar; carpus with subdistal groove, fingers white or horn colored in males, somewhat darker in females, color extending somewhat on palm and terminating in a distinct line; no large tooth at base of major dactyl. Walking legs long and slender.

Measurements.—Carapace: male, length, 21 mm.; width, 27 mm.

Variations.—In individuals 14 mm. wide and smaller, the carpus is much rougher than that described above, has a sharper internal spine, and a longitudinal groove on the upper surface of the palm. In individuals with a carapace width less

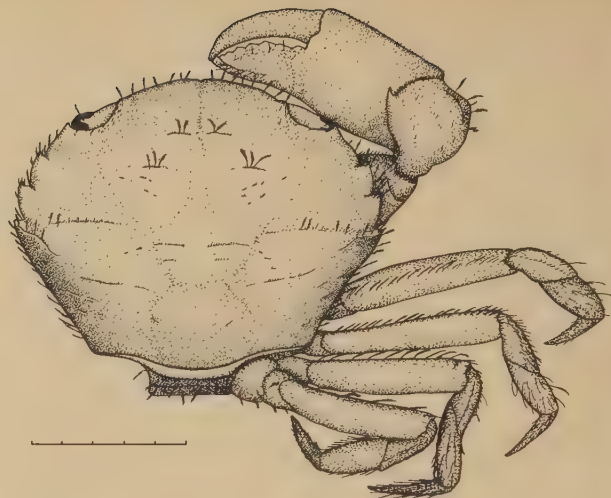


FIGURE 172.—*Neopanope texana texana* (Stimpson). Male in dorsal view, legs of left side not shown, 5 mm. indicated.

than 5 mm., the first and second anterolateral teeth are completely coalesced. Where the ranges of *N. t. texana* and *N. t. sayi* overlap, specimens are often found which share characters of both subspecies (Rathbun, 1930a, p. 370, in part).

Color.—Body mottled gray; a roughly W-shaped grayish configuration on anterior half of carapace with its anterior points located in midline and behind orbits, and a less definite continuation of this figure extending toward anterolateral borders; hands of chelipeds mottled gray, fingers with light tips; walking legs with narrow gray cross bands alternating with lighter ground color.

Habitat.—Most abundant in shallow water where bottom is soft and there is vegetation (Wass, 1955). Low tide to 28 fathoms.

Type locality.—St. Josephs Island, Tex.

Known range.—York River, Va., via Florida Keys and Gulf coast to Laguna Madre, Tamaulipas, Mexico.

Remarks.—Ovigerous females have been reported in March from Florida (Rathbun, 1930a), and they are known from North Carolina in July and August.

Neopanope texana sayi (Smith)

Figures 173, 183G

Panopeus sayi Smith, 1869a, p. 284.

Neopanope texana sayi: Hay and Shore, 1918, p. 438, pl. 34, fig. 8.—Rathbun, 1930a, p. 369, text-fig. 58, pl. 168, figs. 3-4 (rev.).

Neopanope texana nigrodigita Rathbun, 1934, pp. 3-4, illus.

Recognition characters.—Carapace subhexagonal, length contained in width about 1.3 to 1.4 times, greatest width at fifth pair of anterolateral teeth, quite convex; carapace minutely granulate, and lightly pubescent especially near anterior and lateral regions. Five anterolateral teeth, first two coalesced and separated by a shallow sinus, third and fourth larger and directed forward, fifth smaller and directed somewhat outward; each of last two teeth with an oblique ridge extending inward and backward. Front with small median notch, each half only slightly sinuate, with whole forming a much flattened curve extending from eye to eye.

Chelae barely unequal, smooth, dissimilar; carpus and merus with a shallow groove parallel to distal margin, and usually a blunt internal spine; major dactyl without large basal tooth, fingers of minor chelae not spoon shaped.

Resembles *Eurypanopeus depressus*.

Measurements.—Carapace: length, 17 mm.; width, 23 mm.

Variations.—Where the ranges of *N. t. texana* and *N. t. sayi* overlap, specimens are often found which share characters of both subspecies (Rathbun, 1930a, p. 370, in part).

Color.—Carapace a dark, slaty bluish green, brown or buff, with dark reddish-brown speckles on yellowish background, or bluish purple on gray background, especially on anterior portion of carapace and upper portion of chelae; outer face of chelae yellowish gray; fingers dark or black, color extending extensively on palm, tips light.

Habitat.—Most studies indicate greatest abundance on mud bottoms, though the form occurs in other situations as well, and in the Chesapeake area in a salinity range of 14.66 to 31.62 ‰ in a dry year. Low-tide mark to 15 fathoms.

Type localities.—New Haven, Conn., and Cape Cod, Mass.

Known range.—Miramichi Bay, Prince Edward Island and Cape Breton Island, New Brunswick, Canada (Bousfield, 1956), to eastern Florida. Introduced, Swansea, Wales (Naylor, 1960).

Remarks.—Rathbun's subspecies *N. t. nigro-digita* is here regarded as conspecific with *N. t. texana* on the basis of examination of a series of specimens in the Charleston Museum. Rathbun (1930a) reported the largest male on record as 27.2 mm. wide.

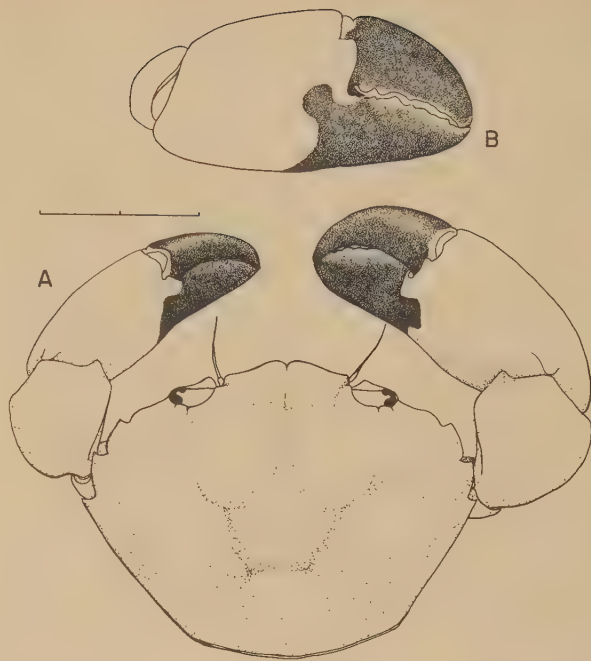


FIGURE 173.—*Neopanope texana sayi* (Smith). A, male in dorsal view, walking legs not shown; B, large chela in frontal view; 10 mm. indicated.

Ovigerous females have been taken from April in South Carolina (Lunz, 1937a) to October in Chesapeake Bay. Cowles (1930) found young individuals during fall, winter, and spring in Chesapeake Bay, and concluded that juveniles reach maturity the first summer after hatching. Ryan (1956) summarized the work of Hyman (1925) on zoeal and megalops stages, and gave some data on size at maturity. He concluded that mature females ranged in width from 6.1 to 18.7 mm.

Chamberlain (1957, 1961) discussed development time and stages in detail. He found development limited to four zoeal stages (sometimes preceded by a brief prezoeal stage) and one megalops stage. Developmental time varied with temperature (14 days at 30° C., 27 at 21° C.) and with food. Larvae matured most rapidly when fed *Artemia salina* nauplii, did moderately well on *Artemia* and algae, but did not transform at all when fed pure algae.

McDermott and Flower (1953) considered this form to be the most abundant mud crab in Delaware Bay, but within the area studied it was more common on oyster beds than in littoral or low-

salinity areas. They found (also McDermott, 1960) that *N. t. sayi* readily preys on *Balanus improvisus*. Farther north, Landers (1954) reported the crab abundant in Narragansett Bay where it is a serious predator on young *Mercenaria mercenaria*. Ryan (1956) found the form widely distributed in Chesapeake Bay, but apparently not so abundant as in the more northern bays. Here it ranged in depth from 2 to 25 fathoms (Rathbun, 1930a, in part), depths similar to those reported by Sumner, Osburn, and Cole (1913a, b) for the Woods Hole region.

Genus *Leptodius* Milne Edwards, 1863

Rathbun, 1930a, p. 296.—Hemming, 1958b, p. 33.

Leptodius agassizii Milne Edwards

Figures 174, 183H

Leptodius agassizii Milne Edwards, 1880, p. 270, pl. 49, fig. 3.—Hay and Shore, 1918, p. 441, pl. 34, fig. 6.—Rathbun, 1930a, p. 307, pl. 141, figs. 4–5 (rev.).

Recognition characters.—Carapace broad, sub-oval, flattened, and finely granulate posteriorly, conspicuously sculptured anteriorly; regions lobulate, with coarse granules and fine scattered hairs along front margin of lobules. Frontal margin transversely grooved, appearing double; upper margin less pronounced than lower, with groove extending across from orbit to orbit, both edges of groove and orbital margin granulate. Of five anterolateral teeth only last two or three well developed, sharp, and turned forward; second tooth, and sometimes third, triangular and obtuse, first (outer orbital angle) represented by an elevated mass of granules.

Chelipeds unequal; larger one with strong, blunt-tipped fingers; smaller one with more slender, more acute, and more conspicuously grooved fingers showing tendency to be spoon shaped at tips; fingers dark, both hands with upper and outer surfaces granulate and tuberculate and with tubercles arranged in rows; carpus strong, with a sharp internal spine, sometimes a double spine, and with many irregular, granulate rugae above. Walking legs granulate and hairy.

Measurements.—Carapace: male, length, 8 mm., width, 12 mm.; ovigerous female, length, 20 mm., width, 31 mm.

Variations.—Small specimens from near Beaufort, N.C., have the last three anterolateral teeth well developed, but a series in the U.S. National

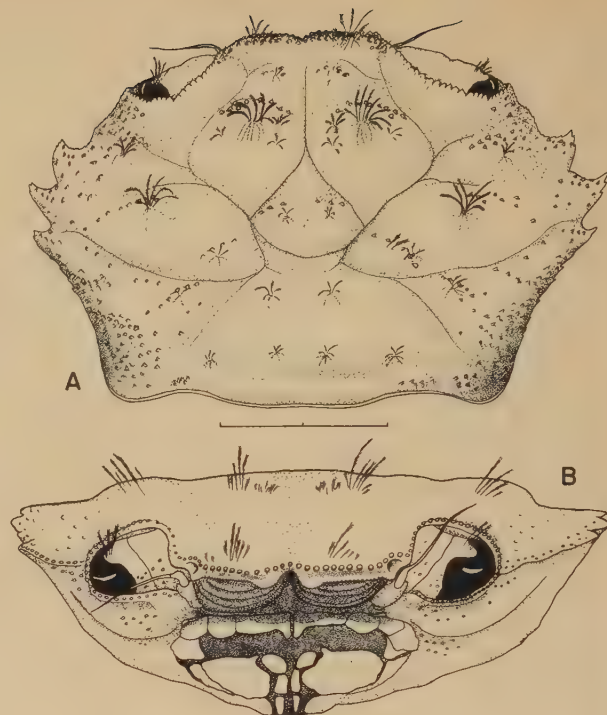


FIGURE 174.—*Leptodius agassizii* Milne Edwards. A, carapace in dorsal view; B, carapace in frontal view; 2 mm. indicated.

Museum from Pensacola, Fla., shows that the number of these spines may be reduced to two in larger individuals.

Color.—After a short preservation in alcohol, light red, fingers black.

Habitat.—This species has been taken from coral rock, sponges, and on sandy bottom. Approximately 6 to 45 fathoms.

Type locality.—Florida Reefs, 12 to 18 fathoms.

Known range.—Cape Hatteras, N.C., to Pensacola, Fla.; Virgin Islands.

Remarks.—Ovigerous females are known from April to November in various parts of the range.

Genus *Micropanope* Stimpson, 1871

Rathbun, 1930a, p. 426.—Hemming, 1958b, p. 34.

KEY TO SPECIES IN THE CAROLINAS

- a. Last lateral tooth of carapace obsolescent, carapace rough, legs spinulose.....*sculptipes* (p. 193).
- aa. Last lateral tooth of carapace small but easily discernible.
 - b. Second lateral tooth present, last lateral tooth denticiform, not spinose; outer surface of hand somewhat rugose.....*xanthiformis* (p. 193).

bb. Second lateral tooth absent or fused with first; outer surface of hand rough with large beadlike granules.-----*nuttingi* (p. 194).

***Micropanope sculptipes* Stimpson**

Figure 175

Micropanope sculptipes Stimpson, 1871a, p. 140.—Rathbun, 1930a, p. 428, pl. 178, figs. 1-3 (rev.).

Recognition characters.—Carapace naked, distinctly areolated; anterior and anterolateral regions somewhat roughened in front with small, sharp, toothlike tubercles partially disposed in lines. Anterolateral teeth sharp, denticulate, fifth (last) obsolescent, first and second almost entirely fused. Frontal lobes abruptly deflexed, with convex outline; margin thin, minutely crenulate, with slight furrow above it. A small tubercle on subhepatic region below second anterolateral tooth.

Chelipeds granulate above; carpus with granules arranged more or less in raised reticulated rugae, inner margin denticulate and with a sharp spine; hand with double denticulate crest above and with minute granules on outer surface showing tendency to arrangement in rows, becoming obsolete in distal lower half of major chela, upper part of inner surface granulate; fingers grooved, with a thin superior crest on dactyls. Walking legs with minute spines above forming two rows on carpus.

Measurements.—Carapace: male, length, 4 mm.; width, 6 mm.

Habitat.—Fifteen to 101 fathoms.



FIGURE 175.—*Micropanope sculptipes* Stimpson. Animal in dorsal view, legs of left side not shown, 2 mm. indicated.

Type locality.—Florida Keys.

Known range.—South Carolina to Port Aransas, Tex.; West Indies to Barbados.

***Micropanope xanthiformis* (Milne Edwards)**

Figures 176, 183I

Panopeus xanthiformis Milne Edwards, 1880, p. 353, pl. 53, figs. 4-4b.—Rathbun, 1930a, p. 442, pl. 180, figs. 7-8 (rev.).

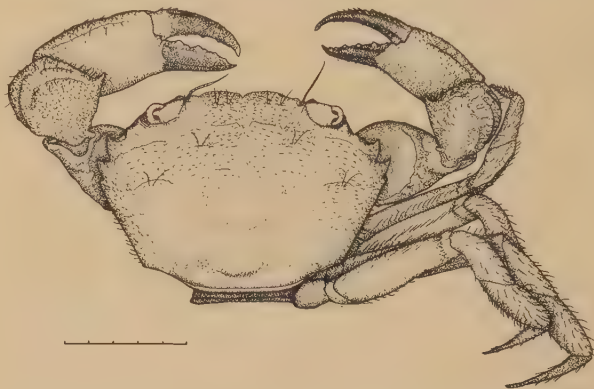


FIGURE 176.—*Micropanope xanthiformis* (Milne Edwards). Animal in dorsal view, walking legs of left side not shown, 5 mm. indicated.

Recognition characters.—Carapace depressed, regions well defined, with depressed coarse granulations on anterior and anterolateral portions, an oblique ridge on hepatic region. Five anterolateral teeth with granulate margins; second tooth small, blunt, obsolescent in young but considerably larger than first in adults; third and fourth teeth large, acute; fifth tooth small and pointed. Front slightly deflexed, shallow, lobes separated by a narrow fissure; margin sinuous, outer corner rectangular. A slight subhepatic elevation formed by a number of granules.

Chelipeds rugose with coarser granules than on carapace; merus with a row of spines above; carpus with a deep distal groove and two inner spines, one above other, upper one largest. Chelae roughened proximally and on upper portion, roughness more extensive on minor chela; fingers deeply grooved, major dactyl with large basal tooth. Walking legs long, slender; merus with row of spines above, other articles spinulose.

Measurements.—Carapace: male, length, 7 mm.; width, 10 mm.

Color.—"Anterior portion of carapace light yellowish orange. Fingers of major chela brownish black, of minor chela black. Spines and tu-

bercles of both chelipeds light salmon." (Rathbun, 1930a.)

Habitat.—Various types of bottom in deeper water; 7.5 to 182 fathoms.

Type locality.—Off Grenada.

Known range.—Cape Hatteras, N.C.; Florida through Gulf of Mexico and West Indies to Cabo Frio, Rio de Janeiro, Brazil; Yucatan.

Remarks.—Ovigerous females are known in June and August from Florida, and in October from North Carolina (Rathbun, 1930a, in part).

***Micropanope nuttingi* (Rathbun)**

Figures 177, 183J

Xanthias nuttingi Rathbun, 1898, p. 271, pl. 4, fig. 1.

Micropanope nuttingi: Rathbun, 1930a, p. 450, fig. 74 (rev.).

Recognition characters.—Carapace suboval, convex from front to back, nearly flat transversely; regions distinct, anterior half rough with squamose tubercles. Second normal anterolateral tooth completely united with small first tooth; three remaining teeth sharp pointed, posterior one smallest. Front convex, bilobulate, with granulate margins separated by a V-shaped sinus, outer angle of each lobe subrectangular.

Chelipeds heavy, quite unequal; merus spinulose on upper edge; carpus covered with beadlike tubercles, with a deep distal groove, and an inner angular eminence tipped with a spinule and a second spinule below. Females with whole outer surface of both chelae tuberculate. Major chela of males with upper and approximately two-thirds of outer surface beaded, tuberculate; lower third and distal extremity smooth and shining; fingers broad, not gaping, brown with light tips, color of immovable finger not continued on palm and ending in a line with articulation of dactyl; dactyl with large basal tooth. Minor chela almost entirely tuberculate, growing less so toward distal and lower margins; upper margin with longitudinal groove, fingers deeply grooved. Upper margin of walking legs tuberculate or granulate.

Measurements.—Carapace: male, length, 4 mm.; width, 6 mm.

Color.—"In alcohol, speckled with blue; larger patches of blue on anterior gastric and cardiac region." (Rathbun, 1930a.)

Habitat.—Has been taken from boulder-covered beach, from *Porites* clumps and *Halimede* (U.S. National Museum records); shallow water to 100 fathoms.

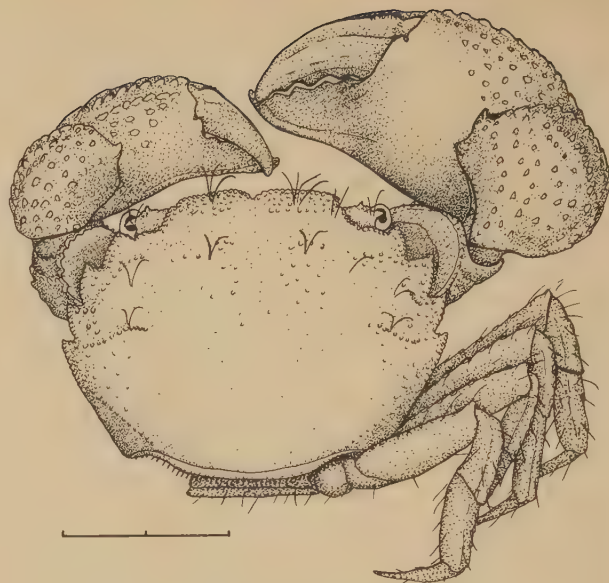


FIGURE 177.—*Micropanope nuttingi* (Rathbun). Animal in dorsal view, walking legs of left side not shown, 2 mm. indicated.

Type locality.—Bahama Banks.

Known range.—Cape Hatteras, N.C., through Gulf of Mexico and West Indies to Cape São Roque, Rio Grande do Norte, Brazil.

Remarks.—Ovigerous females have been taken in July in Florida.

Genus *Eurypanopeus* Milne Edwards, 1880

Rathbun, 1930a, p. 403.

KEY TO SPECIES IN THE CAROLINAS

- a. Fingers of both chelae with acute tips, not spooned
abbreviatus (p. 194).
- aa. Fingers of minor chela spoon-shaped at tip
depressus (p. 195).

***Eurypanopeus abbreviatus* (Stimpson)**

Figures 178, 183K

Panopeus abbreviatus Stimpson, 1860a, p. 211.

Eurypanopeus abbreviatus: Rathbun, 1930a, p. 404, text-fig. 63, pl. 172, figs. 1-2 (rev.).

Recognition characters.—Carapace approximately two-thirds broader than long, moderately convex in two directions, naked above, granulate and uneven on front and along anterolateral border, smooth and polished elsewhere; areolations slightly but distinctly indicated, a number of well-marked rugae among granules. Front strongly deflexed, four-lobed, median lobes prominent, separated by a V-shaped notch. Antero-

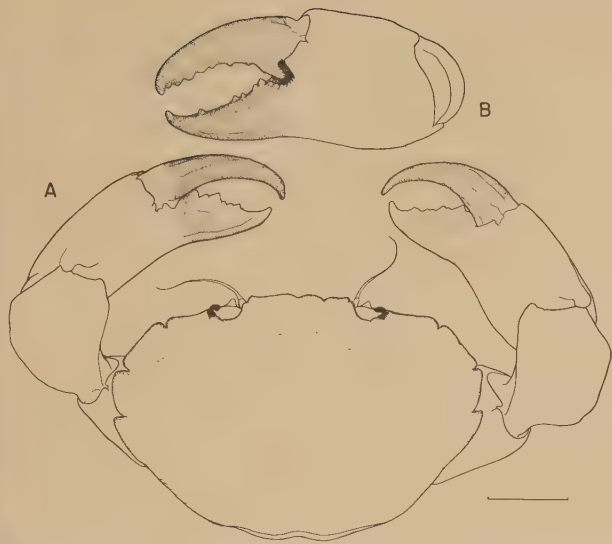


FIGURE 178.—*Eurypanopeus abbreviatus* (Stimpson). A, male in dorsal view, walking legs not shown; B, right chela in frontal view; front with anomalous notch to right of midline; 5 mm. indicated.

lateral margin thin, divided into four lobes, first and second teeth coalesced, separated by a slight concavity; third tooth obtuse; fourth with outer margin longitudinal or nearly so; fifth subtriangular, directed outward. A low granulated swelling below interval between first two teeth.

Chelipeds quite unequal in males; carpus with blunt internal tooth; fingers slender, pointed, widely gaping in major chela; fitting closely in minor, tips crossing in both; major dactyl with a large basal tooth, color of fingers not extending on palm.

Measurements.—Carapace: male, length, 14 mm.; width, 22 mm.

Color.—Yellowish or brownish above, front margin of carapace and chelipeds roseate or tinged with bluish purple; fingers black with paler tips. Brazilian specimens with a number of large dark spots on upper half of chelipeds.

Habitat.—Specimens have been found near shore on oysterbeds, under rocks, and among sponges and bryozoan growth; shore and shallow water to unknown depth.

Type locality.—Barbados, British West Indies.

Known range.—South Carolina, through West Indies and Gulf of Mexico to State of Santa Catarina, Brazil.

Remarks.—Ovigerous females are known from April to November in the West Indies, and

August to November in southern Brazil (Rathbun, 1930a, in part).

Eurypanopeus depressus (Smith). Flat mud crab

Figures 179, 183L

Panopeus depressus Smith, 1869a, p. 283.

Eurypanopeus depressus: Hay and Shore, 1918, p. 437, pl. 34, fig. 4.—Rathbun, 1930a, p. 410, text-fig. 65, pl. 173, figs. 3–4 (rev.).

Recognition characters.—Carapace transversely oval, approximately three-fourths as long as wide, flattened posteriorly, convex in anterior half; areolations well defined, finely granulate, with several pairs of transverse rows of granulations. Anterolateral teeth four, outer margins granulate; first two teeth coalesced to form broad lobe with slightly sinuate margin; third tooth blunt; fourth and fifth spines tipped, pointing obliquely upward and forward. Front nearly straight, median notch small or absent.

Chelipeds dissimilar and quite unequal. Smaller one more rugose than larger and with margins of fingers nearly straight and opposable for a considerable distance, with opposed margins of tips thin edged and hollowed out—"spoon shaped." Larger cheliped with nearly smooth articles, hand heavy and inflated; dactyl strongly curved, obscurely toothed at base, and meeting immovable finger only at tip; internal tooth of carpus tipped with small spinule; in unworn condition both fingers show indication of spoonlike flattening.

Measurements.—Carapace: length, 14 mm.; width, 20 mm.

Variations.—Ryan (1956) described a persistent, central, oval, blood-red spot or structure on the inner surface of the ischium of the third maxillipeds of both sexes. The spot is often two-thirds the length of the article, with its surface raised slightly above the surface of the ischium. When pressure is applied, the hard spot cracks and is easily dissected out. A similar spot has been noted on *P. herbstii*.

The normal male abdomen is narrow with the third, fourth, and fifth segments fused. A few variant males have wide abdomens with seven segments, resembling females.

Color.—Mottled grayish olive or dark olive brown, especially on upper surfaces of chelipeds and anterior portions of carapace; fingers dark brown with dark color of immovable finger extended on palm; body and legs light colored underneath.



FIGURE 179.—*Eurypanopeus depressus* (Smith). A, animal in dorsal view, walking legs not shown; B, large chela in frontal view; 5 mm. indicated.

Habitat.—In Chesapeake Bay, Ryan (1956) found this species in greater abundance on oyster bars than any other species of mud crab, and evidence was presented showing a positive relationship between presence of oyster shells and this species. Others have noted a similar habitat preference (Lunz, 1937a). In the bay, the depth range was 1 to 15 fathoms (Cowles, 1930, in part), and the salinity range occupied was 4.5 to 20.4‰. Elsewhere the species occurs from shore to 26 fathoms.

Type locality.—New Haven, Conn.

Known range.—Massachusetts Bay through Florida (east and west coasts) to Texas; Bermuda; West Indies.

Remarks.—Ryan (1956) gave much detail on the life history of this species in Chesapeake Bay. Ovigerous females were collected from June to September. Elsewhere, Rathbun (1930a) and Lunz (1937a) reported such females in April from Virginia and South Carolina, September

from Mississippi and the Leeward Islands, November and February from Florida. Zoeal stages have been studied by Hyman (1925) from plankton tows made in the Beaufort, N.C., area. Costlow and Bookhout (1961b) worked out the entire larval and postlarval history in captivity and illustrated four zoeal stages and a single megalops stage. Immature males from Chesapeake Bay ranged in width from 3.2 to 6 mm. and females from 3.6 to 6.4 mm.

Maturity was considered to be attained at widths of 5.1 to 6 mm. in males, and 5.5 to 6.4 mm. in females. The mature individuals range widely in size, up to a width of 21 mm. for females, and ovigerous females show a range of 6 to 17 mm. Such a broad range of sizes among mature individuals suggested to Ryan that growth and molting continue after maturity is reached. Maturity may be reached in the first summer after eggs have hatched.

McDermott (1960) found that *E. depressus* is a predator on oyster spat in southern New Jersey but not so serious a pest as *P. herbstii*.

Genus *Panopeus* H. Milne Edwards, 1834

Rathbun, 1930a, p. 333.

KEY TO SPECIES IN THE CAROLINAS

- a. Dark color of immovable finger continued more or less on outer surface of palm, especially in males; no distal groove on carpus of chelipeds.....*herbstii* (p. 196).
- aa. Dark color of immovable finger not continued on outer surface of palm; carpus of chelipeds with shallow groove parallel to distal margin...*occidentalis* (p. 198).

Panopeus herbstii H. Milne Edwards. Common mud crab

Figures 180, 183M

Panopeus herbstii H. Milne Edwards, 1834, p. 403.—Hay and Shore, 1918, p. 437, pl. 34, fig. 9.—Rathbun, 1930a, p. 335, text-figs. 52–53, pl. 156, figs. 1–3; pl. 157, figs. 1–3 (rev.).

Recognition characters.—Carapace approximately two-thirds as long as wide, regions well marked, surface sparingly granulate. Antero-lateral margins with five teeth; first two teeth coalescent; third and fourth larger, prominent, and with arcuate outer margins and acute tips; fifth smaller, acute at tip and with outer margin straight. A transverse ridge extending inward from fifth tooth, and a shallow groove from fourth tooth. Front wide, not produced, with narrow median fissure; anterior margin of each half sinuous. Male abdomen with sides of

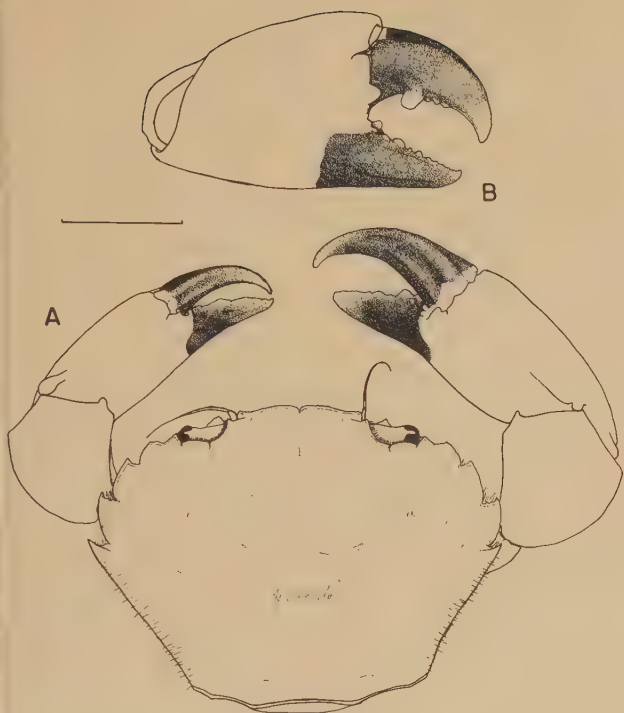


FIGURE 180.—*Panopeus herbstii* H. Milne Edwards. A, animal in dorsal view, walking legs not shown; B, right chela in frontal view; 5 mm. indicated.

penultimate segment nearly parallel; terminal segment broader than long, rounded at tip.

Chelipeds heavy, finely granulate; carpus without groove on superior surface and with a blunt internal spine; hands unequal and dissimilar, large one with dactyl curved and strongly toothed at base, dactyl of smaller more nearly straight; fingers dark, with color extending somewhat on palm.

Measurements.—Carapace: male, length, 26 mm.; width, 38 mm.

Variations.—Rathbun (1930a) separated this species into a number of forms on the basis of structural characteristics but considered these the result of response to environment rather than genetic differences. Intermediates may occur in any locality; thus, the forms are not always easily separated.

Ryan (1956) described a persistent, central, oval, red spot or structure on the inner surface of the ischium of the third maxillipeds of both sexes. Mrs. Peggy Keney of the U. S. Fish and Wildlife Service Bureau of Commercial Fisheries, Biological Laboratory, Beaufort, N.C., found this

spot to occur on 100 percent of males and 55 percent of females in the Beaufort area. A sample of 596 specimens was examined.

Habitat.—Depth distribution for the species ranges from the intertidal zone to 12 fathoms. Ryan (1956) found the species to be rare in Chesapeake Bay in a salinity range of 13.95 to 19.04‰. The depth distribution there was 2 to 6 fathoms and at each collection spot the bottom was composed of soft mud with few oyster shells. McDermott and Flower (1953) found the species common on oyster beds in Delaware Bay, where it commonly cracks and eats small oysters and the barnacle *Balanus eburneus*. The toadfish was considered a common predator.

In North Carolina and South Carolina, this is one of the most common crabs of estuarine regions, found wherever the bottom is muddy or covered with shells or stones. In some localities along edges of the higher marshes, it is found in burrows and is frequently associated with *Sesarma reticulata* and *Uca minax*.

In the West Indies, collections have been made from mangrove roots, sponges, and coral reefs.

Type locality.—North America.

Known range.—Boston, Mass., to State of Santa Catarina, Brazil; Bermuda.

Remarks.—This common xanthid crab has a fossil record dating from the Miocene in North America, and the genus *Panopeus* has a record extending from the Eocene to the present (Rathbun, 1935).

Ovigerous females are known virtually the year around in Florida. They are known through late spring and summer in the Carolinas, in July in Maryland, February to September in various parts of the West Indies, and August to October in southern Brazil.

Ryan (1956) gave carapace widths of mature males as 8.3 to 37.3 mm., and of mature females as 21.6 to 27.8 mm. A specimen 45 mm. wide was found at Beaufort, N.C., in 1960 (Mrs. Keney, personal communication), and Wass (1955) reported a male 55 mm. wide.

Costlow and Bookhout (1961a) reviewed early descriptions of larvae and described and illustrated four zoeal and one megalops stage reared in the laboratory.

Costlow, Bookhout, and Monroe (1962) reared the larval stages under 12 different conditions of

salinity and temperature. Eggs were maintained in salinities of 12.5, 20.1, 26.5, and 31.1‰ and all larvae hatched as first stage zoeae. Succeeding stages showed higher percentages of survival under different conditions, with shortest development time in the highest salinity. The lowest salinity tested did not permit development to be completed. In addition, low temperature affected duration of all larval stages and mortality of some stages. Larval development was completed to first crab in 48–52 days at 20° C., in 18–28 days at 30° C. From data, the effects of salinity and temperature on mortality of larval stages were projected by statistical methods over a wide range of combinations. The hypothesis is presented that the effect of temperature on successive larval stages limits the productive spawning period. Low temperatures favor the spring brood of larvae [in these latitudes], prolonging larval development until warmer water produces favorable conditions for the megalops stage. Larvae hatched in fall are not so favored and mortality in late zoeal and megalops stages would be high.

In a study of the relationship of habitat to oxygen consumption by estuarine crabs, Ayers (1938) found *P. herbstii* to be intermediate in a scale of partial adaptation of the respiratory mechanisms to life in air. Teal (1959) found this species active on Georgia marshes when the tide was high or the sky cloudy. When the marsh was exposed, it was found in burrows, usually near the top, in air or water. Among various marsh crabs studied (see remarks, *Uca minax*) only *P. herbstii* was active at temperatures below 12° C. Respiration in this crab was most affected by reduced oxygen pressure among species tested, showing a rate reduction of 90 percent at 4 mm. Hg.

Menzel and Nichy (1958) found that *P. herbstii* and *Menippe mercenaria* are the only xanthids large enough to kill significant numbers of adult oysters. McDermott (1960), studying predatory activities of xanthid crabs on oyster beds in New Jersey, found that *P. herbstii* destroyed 1- and 2-year-old oysters at a rate of 0.15 oysters per crab per day. The crab also preyed actively on oyster spat as well as barnacles (*Balanus improvisus*). He concluded that *P. herbstii* is potentially the most destructive of the five species of mud crabs occurring on New Jersey oyster beds.

Panopeus occidentalis Saussure

Figures 181, 183N

Panopeus occidentalis Saussure, 1857, p. 502.—Rathbun, 1930a, p. 348, text-fig. 55; pl. 161, figs. 1–3 (rev.).

Recognition characters.—Similar to *Panopeus herbstii*, but differing in having more convex carapace, especially in gastric region; front narrow, advanced; second anterolateral tooth usually narrower and separated by deeper sinus from first tooth, third to fifth teeth thicker, more prominent and widely separated, third one blunt, forming almost a right angle at tip; abdomen of male wider, sides of penultimate segment not parallel, narrowed toward proximal end.

Carpus of chelipeds with groove parallel to distal margin, sometimes rugose; dark color of immovable finger not continued on palm. Walking legs somewhat longer and more slender.

Measurements.—Carapace: male, length, 23 mm.; width, 33 mm. Smaller than *P. herbstii*.

Variations.—There is considerable variation even in a single lot of specimens. The carapace may be smooth and shining, or with light, granulate, transverse lines; the second anterolateral tooth may be small, subacute, and similar to the first rather than broadly rounded and large; the female abdomen may have sides of the sixth segment parallel instead of converging slightly toward the proximal end. Variations in teeth of the anterolateral border were noted in 12 percent of females studied by de Oliveira (1940). In these the first, second, and third teeth of one side were depressed, giving the impression of but one sinuous tooth while those of the other side were normal.

This species, like *P. herbstii*, has been divided into two environmental forms (typical and serate), and both occur in the Carolinas (Rathbun, 1930a).

Color.—Carapace dull yellow spotted with brown and red; legs yellow with brown maculations and speckles on chelipeds; walking legs with brown or rose streaks. De Oliveira (1940) gave color of the species in Brazil as: carapace dark yellow with red blotches or chocolate varying in tone; legs same color but spotted with reticulated points, points of fingers chocolate to almost black; body yellow ventrally, legs yellow to grayish; some rare specimens completely yellow.

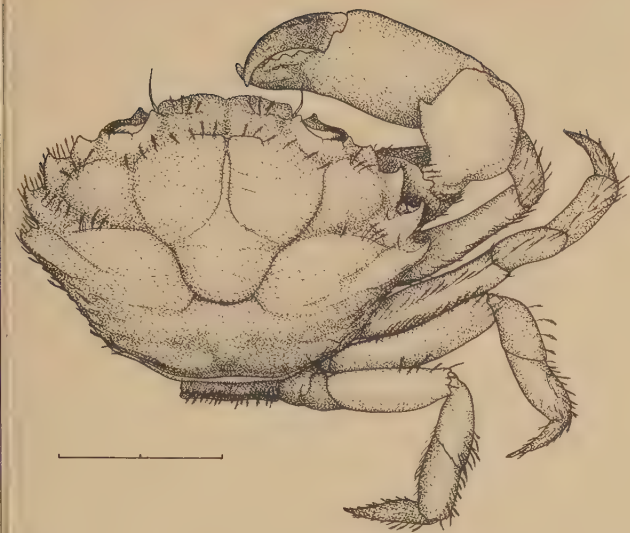


FIGURE 181.—*Panopeus occidentalis* Saussure. Animal in dorsal view, legs of left side not shown, 10 mm. indicated.

Habitat.—This species has been found among rocks, mangrove roots, sponges, ascidians, and seaweed, and on pilings of piers along shore; shore to 10 fathoms.

Type locality.—Guadeloupe.

Known range.—North Carolina to State of Santa Catarina, Brazil; West Indies and Bermuda.

Remarks.—De Oliveira (1940) reported in some detail on the natural history of this species where it occurs in the vicinity of the Ilha Pinheiro, near Rio de Janeiro, Brazil. The species is primarily crepuscular or nocturnal and is found living chiefly in ditches, between and beneath stones, and among mangrove roots, often burrowing to a depth of 30 cm. Both sexes were found together except when the eggs were deposited, and then females were not so often seen. Molting individuals and copulating pairs were rarely found.

Mating pairs were found from November to December, and on one occasion in water of 22 ‰ at 22° C. Periods of egg deposition extended from January to May, and again from July to August (September, Rathbun, 1930a). (In the Caribbean area ovigerous females are known from January to July, U.S. National Museum records.) The seldom-seen ovigerous females bore dark, chocolate colored eggs. Such females showed a range in carapace width from 13.3 mm. to 35.2

mm., and bore 3,000 to 70,000 eggs, depending on size. Females were observed to aerate and clean the eggs in water at low tide in the evening. Eggs in the laboratory hatched in about 15 days. Molting of females followed hatching of eggs.

Young of the species were found throughout the year, as others have noted. One large male measured 48.2 mm. [width], though the average dimension for the typical form was 27.7 mm. long by 40.5 mm. wide; for the serrate form, 19.9 mm. long by 27.5 mm. wide.

The species was believed to have few natural enemies. Material from the gut was found to consist of a variety of plant and animal matter. In addition to the ecological discussion, de Oliveira gave a number of observations on autotomy and its effect on movement and behavior.

Genus *Eurytium* Stimpson, 1859

Rathbun, 1930a, p. 422.—Hemming, 1958b, p. 32.

Eurytium limosum (Say)

Figures 182, 183 O

Cancer limosa Say, 1818, p. 446.

Eurytium limosum: Hay and Shore, 1918, p. 438, pl. 35, fig. 7.—Rathbun, 1930a, p. 423, pl. 176, figs. 1–2 (rev.).

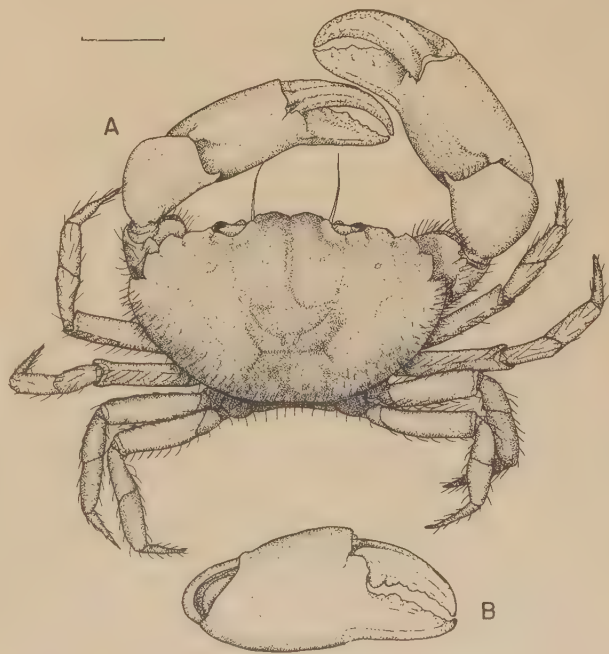


FIGURE 182.—*Eurytium limosum* (Say). A, animal in dorsal view; B, large chela in frontal view; 10 mm. indicated.

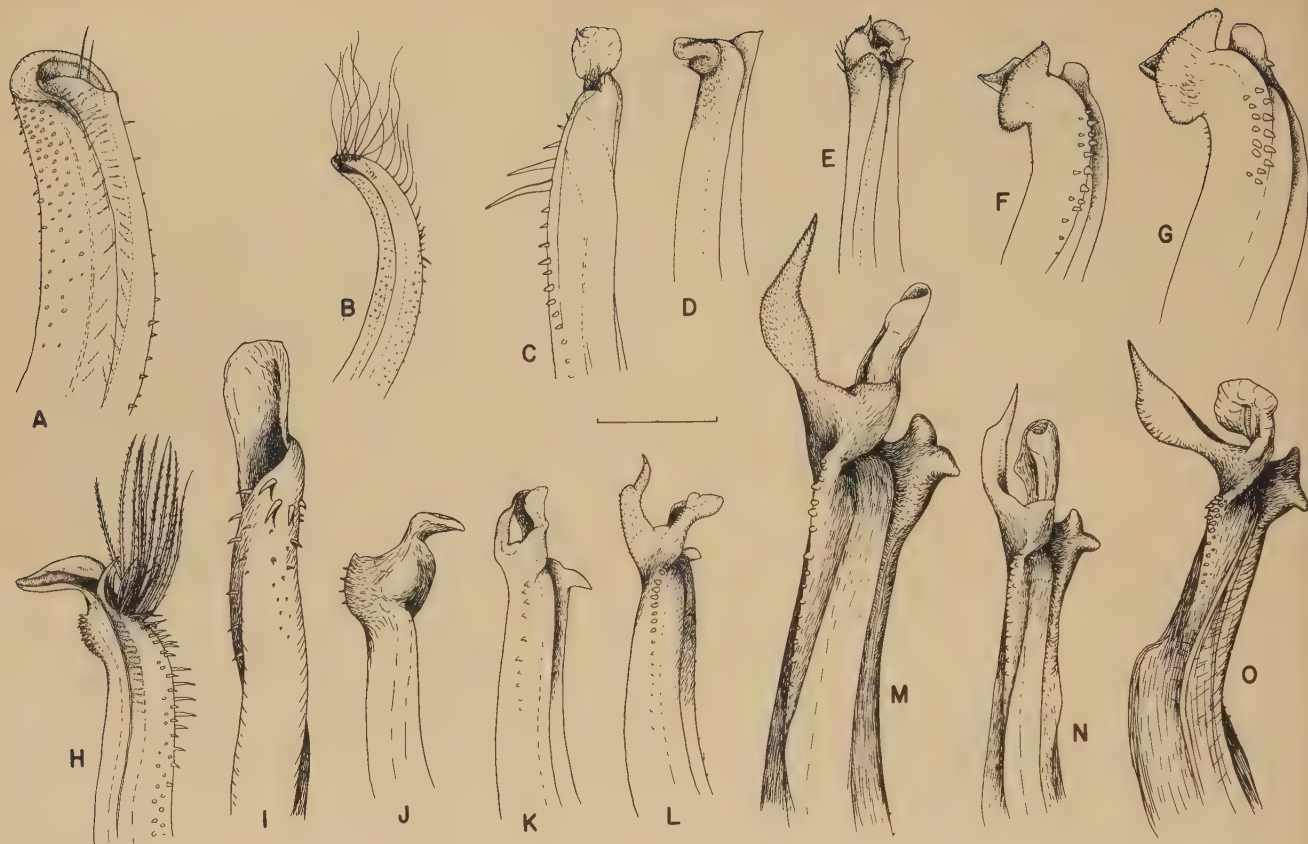


FIGURE 183.—Tips of right first pleopods of male xanthids; A, *Glyptoxanthus erosus* (Stimpson), medial view; B, *Carpaporus papulosus* Stimpson, medial view; C, *Rhithropanopeus harrisii* (Gould), medial view; D, *Hexapanopeus angustifrons* (Benedict and Rathbun), medial view; E, *Hexapanopeus paulensis* Rathbun, medial view; F, *Neopanope texana texana* (Stimpson), medial view; G, *Neopanope texana sayi* (Smith), medial view; H, *Leptodius agassizii* Milne Edwards, medial view; I, *Micropanope exanthiformis* (Milne Edwards), abdominal view; J, *Micropanope nuttingi* (Rathbun), medial view; K, *Eurypanopeus abbreviatus* (Stimpson), medial view; L, *Eurypanopeus depressus* (Smith), medial view; M, *Panopeus herbstii* H. Milne Edwards, medial view; N, *Panopeus occidentalis* Saussure, medial view; O, *Eurytium limosum* (Say), medial view; 0.5 mm. indicated for all figures, except I and J twice this magnification, and O one-half this magnification.

Recognition characters.—Carapace broad, approximately 1.5 times as wide as long, quite convex from front to back, nearly plane from side to side; surface smooth to eye but under a lens finely granulate, granulations coarser near frontal and anterolateral margins. Front approximately one-fourth width of carapace, divided into two lobes by a median notch giving rise to a shallow groove disappearing over gastric region. Orbital margins somewhat elevated; external orbital tooth coalesced with first tooth of anterolateral border, division between these teeth indicated by a shallow notch. Anterolateral teeth with raised margins, second and third teeth rounded at tip, fourth more prominent and subacute.

Chelipeds massive, unequal, and dissimilar, more so in male than in female; merus with coarsely tuberculate superior border and a distal spiniform tooth; carpus with a narrow internal spine, not grooved; fingers pointed, deflexed, with large basal tooth on major dactyl.

Measurements.—Carapace: length, male, 24 mm.; width, 36 mm.

Color.—Carapace brilliant purplish blue, dark gray, or black; carpus and hand bluish; proximal upper half of dactyl pink or purple; remainder of fingers porcelain white; lower portion of chelipeds, and also carpal teeth, yellow or orange; color of fingers not continued on palm.

Habitat.—This primarily tropical species lives in muddy or marshy banks a bit below the high-

tide mark in burrows partially filled with water, among stones at the high-tide mark, in burrows in sand, under stones between tides, and on coral reefs (Rathbun, 1930a). High-tide mark to shallow depths near shore.

Type locality.—"Inhabits shores of the Northern States."

Known range.—Modern records, South Carolina to State of São Paulo, Brazil; Bermuda. Formerly reported from New Jersey (Ryan, 1956).

Remarks.—This species has a fossil record in North America dating from the Miocene of North Carolina and Florida (Rathbun, 1935).

Teal (1959) found this species active on Georgia marshes when the tide was high or the sky cloudy. When the marsh was exposed, it was found in burrows, usually near the top, either in air or water. Respiration rates in water were higher than in air. The species showed internal regulation of metabolism in that it was independent of oxygen tension but not of acclimation to temperature.

Ovigerous females have been reported from Florida in August (Wass, 1955).

Family Goneplacidae

Palp of external maxillipeds articulating at or near anterointernal angle of merus; exognath normal in size, not concealed. Antennular septum a thin plate. Division of orbit into two fossae usually not indicated. Genital ducts of male usually perforating base of last pair of legs, often passing through a groove in sternum.

This group has a general resemblance to the Xanthidae in body shape. Members of the group are all bottom dwellers.

KEY TO GENERA AND SPECIES IN THE CAROLINAS

a. Base of third segment of male abdomen covering whole space between last pair of legs; carapace subquadrate, widest between postorbital angles; anterior border entirely occupied by square-cut front, and orbits formed into long, narrow trenches—*Goneplax hirsuta* (p. 201).

aa. Base of third segment of male abdomen not covering whole space between last pair of legs.

b. Frontoorbital width almost as great as total width of carapace; eyestalks long; carapace subquadrate, posterolateral margins converging

Euryplax nitida (p. 202).

bb. Frontoorbital width from one-half to three-fourths total width of carapace; eyestalks short; anterolateral margins arcuate

Speocarcinus carolinensis (p. 202).

Genus *Goneplax* [Leach, 1814]

Rathbun, 1918b, p. 25.—Hemming, 1958a, p. 32.

Goneplax hirsuta Borradaile

Figure 184

Goneplax hirsuta Borradaile, 1916, p. 99, fig. 11.—Rathbun, 1918b, p. 28, text-fig. 7 (rev.).

Recognition characters.—Carapace approximately two-thirds as long as broad, greatest width between tips of postorbital spines; regions faintly marked except for H-shaped depression in middle. Sides converging backward from prominent, sharp, postorbital spines; armed with sharp spine near postorbital spine. Front almost straight, with low rostral prominence in broad, shallow median notch. Orbital margin sinuous, sloping backward, width of orbit and front nearly equal.

Chelipeds almost equal; merus about two-thirds length of carapace, deep, with a spine a little beyond middle of upper edge; carpus broader than long, with a stout internal spine. Hand longer than remainder of limb; fingers about equal to palm, irregularly toothed, not gaping; external base of hand and distal half of carpus with a long dense tuft of hair, fringe of similar hairs along inner side of merus. Walking legs slender, meri smooth or fringed with light pubescence, distal articles fringed with hairs.

Measurements.—Carapace: male, length, 19 mm.; width, 29 mm.

Habitat.—Forty to eighty fathoms.



FIGURE 184.—*Goneplax hirsuta* Borradaile. A, animal in dorsal view; B, right chela and carpus in outer view; approximately $\times 1.75$ (after Borradaile, 1916).

Known range.—North Carolina to Rio de Janeiro, Brazil.

Remarks.—Ovigerous females have been taken in the Gulf of Mexico off Florida in June (U.S. National Museum records).

Genus *Euryplax* Stimpson, 1859

Rathbun, 1918b, p. 34.—Hemming, 1958b, p. 32.

Euryplax nitida Stimpson

Figure 185

Euryplax nitida Stimpson, 1859, p. 60.—Rathbun, 1918b, p. 34, text-fig. 11, pl. 7 (rev.).

Recognition characters.—Carapace smooth and shining, convex. Front deeply notched on each side at insertion of antennae; interantennal margin nearly straight. Anterolateral margins converging anteriorly, less than half as long as posterolateral margins and armed with three strong teeth including outer orbital. Carapace widest at level of third tooth.

Merus of chelipeds in male with a deep round pit at anterior distal corner of lower surface, pit surrounded by a fringe of long hair, and with a sharp curved spine near distal end of upper surface; carpus with a sharp inner spine and inner surface pilose. Walking legs slender.

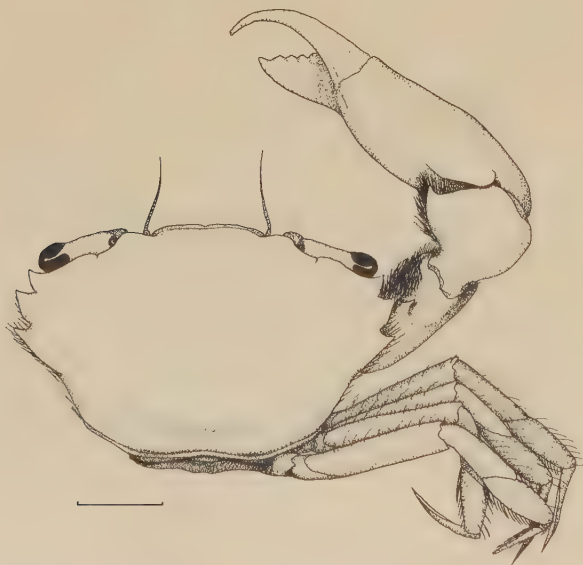


FIGURE 185.—*Euryplax nitida* Stimpson. Male in dorsal view, legs of left side not shown, 5 mm. indicated.

Female with narrower carapace; chelipeds more nearly equal, and merus lacking pit with surrounding hair.

Measurements.—Carapace: male, length, 15 mm.; width, 25 mm.

Color.—Distal half of fingers white (Rathbun, 1918b).

Habitat.—Shallow water to 49 fathoms.

Type locality.—Florida Keys.

Known range.—Off Beaufort, N.C., to Texas; West Indies to St. Thomas; Bermuda.

Remarks.—Ovigerous females have been taken in June from southern Florida.

Genus *Speocarcinus* Stimpson, 1850

Rathbun, 1918b, p. 38.—Hemming, 1958b, p. 37.

Speocarcinus carolinensis Stimpson

Figure 186

Speocarcinus carolinensis Stimpson, 1859, p. 59, pl. 1, figs. 1-3.—Rathbun, 1918b, p. 39, pl. 8, pl. 159, fig. 6 (rev.).

Recognition characters.—Carapace subcylindrical, nearly smooth, punctate, obscurely granulate near margins, pubescent; gastric region and subdivisions well defined. Anterolateral margin with five teeth including outer orbital; second tooth rounded and not always separated from first; last three teeth sharp, well defined. Posterolateral margins parallel. Front approximately one-fourth width of carapace, sinuous, nearly straight, with median emargination. Eyestalks constricted near cornea.

Chelipeds strong, nearly smooth, margins hairy; merus with a strong spine on upper border; carpus granulate internally and with a blunt internal tooth; hand with outer surface smooth, microscopically granulate; dactyl with stout tooth at base. Walking legs with hairy margins.

Measurements.—Carapace: male, length, 23 mm., width, 29 mm.; female, length, 17 mm., width, 27 mm.

Habitat.—"This crab lives in the subterranean galleries excavated in the mud at low-water mark by the *Squilla*, *Callinassa*, and other Crustacea, or by large worms," (Stimpson in Rathbun, 1918b); near low-tide mark to 76 fathoms.

Type locality.—Charleston Harbor, S.C.

Known range.—South Carolina through Gulf of Mexico and West Indies to Surinam.

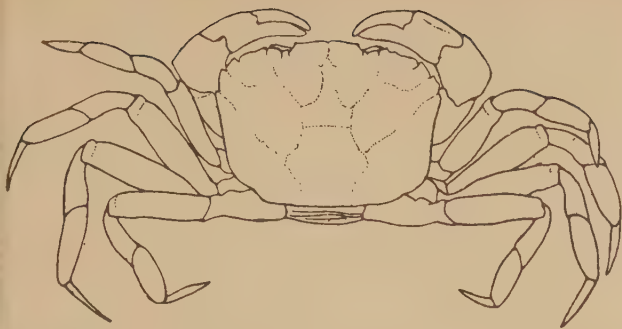


FIGURE 186.—*Speocarcinus carolinensis* Stimpson. Type female in dorsal view (after Rathbun, 1933).

Family Pinnotheridae

Carapace often somewhat membranous. Anterolateral margins entire or very slightly dentate. Front, orbits, and eyestalks very small, cornea often rudimentary. Buccal cavity usually wide, often semicircular in outline. Merus of third maxilliped never quadrate, and never with palp distinctly at anterointernal angle; ischium small, absent, or fused with merus and directed obliquely inward (Rathbun, 1918b).

Small crabs living as commensals or parasites in bivalve mollusks, ascidians, worm tubes, and on or in echinoderms. Free living or migratory stages are occasionally taken in open water.

KEY TO GENERA IN THE CAROLINAS

- a. Dactyls of walking legs simple, acute.
 - b. Third walking leg little, if any, longer than other legs.
 - c. Carapace suborbicular and somewhat membranous in mature female, flattened and firm in hard stage male and female buccal mass subquadrate
Pinnotheres (p. 203).
 - cc. Carapace oval, flattened, and rather firm; buccal mass subtriangular.....*Parapinnixa* (p. 208).
 - bb. Third walking leg longer and stronger than others, often considerably so.....*Pinnixa* (p. 210).
- aa. Dactyls of first, second, and third walking legs bifurcate.....*Dissodactylus* (p. 209).

Subfamily Pinnotherinae

Carapace usually not markedly transverse. Ischium of external maxillipeds either rudimentary or indistinguishably fused with merus to form single piece, usually oblique, occasionally nearly transverse; palp not so large as merus-ischium (Rathbun, 1918b).

Genus *Pinnotheres* Bosc [1801 or 1802]

Rathbun, 1918b, p. 62.—Hemming, 1958b, p. 36.

KEY TO SPECIES IN THE CAROLINAS

Hard-stage males and females

- a. Carapace with a striking pattern of light spots on dark background of pubescence.....*maculatus* (p. 206).
- aa. No striking color pattern.....*ostreum* (p. 203).

Posthard females (and male *maculatus*)

- a. Carapace nearly naked.....*ostreum* (p. 203).
- aa. Carapace covered with a short deciduous pubescence
maculatus (p. 206).

Pinnotheres ostreum Say. Oyster crab

Figures 187, 188, 189

Pinnotheres ostreum Say, 1817, p. 67, pl. 4, fig. 5.—Rathbun, 1918b, p. 66, text-fig. 30; pl. 15, figs. 3–6 (rev.).—Hay and Shore, 1918, p. 443, pl. 35, fig. 9.

Pinnotheres depressum Say, 1817, p. 68.

Pinnotheres depressus: Rathbun, 1918b, p. 79, pl. 17, figs. 1–2 (rev.).

Recognition characters.—Mature female: Carapace subcircular in outline; surface glabrous for most part, smooth, shining, membranous, yielding to touch, convex from front to back and with a broad, shallow, longitudinal depression at each side of cardiac and gastric areas. Lateral margins thick and bluntly rounded; posterior margin broad. Front rounded, slightly produced, covering and concealing eyes. Orbits small, subcircular, anteriorly placed. Antennule large; antenna small, flagellum not so long as diameter of orbit. Buccal mass roughly quadrangular in outline but bent into broad crescentic arch, short anteroposteri-

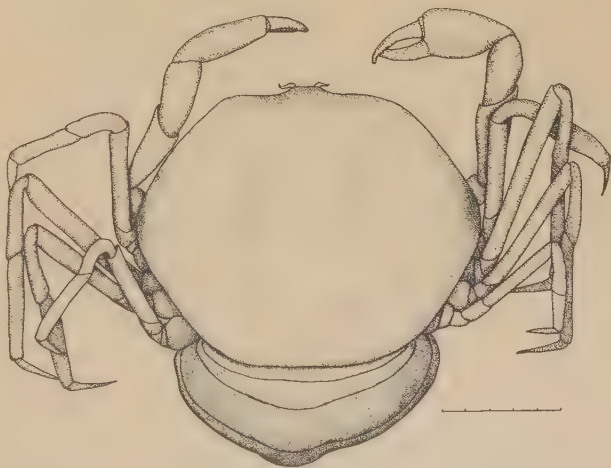


FIGURE 187.—*Pinnotheres ostreum* Say. Mature female in dorsal view, 5 mm. indicated.

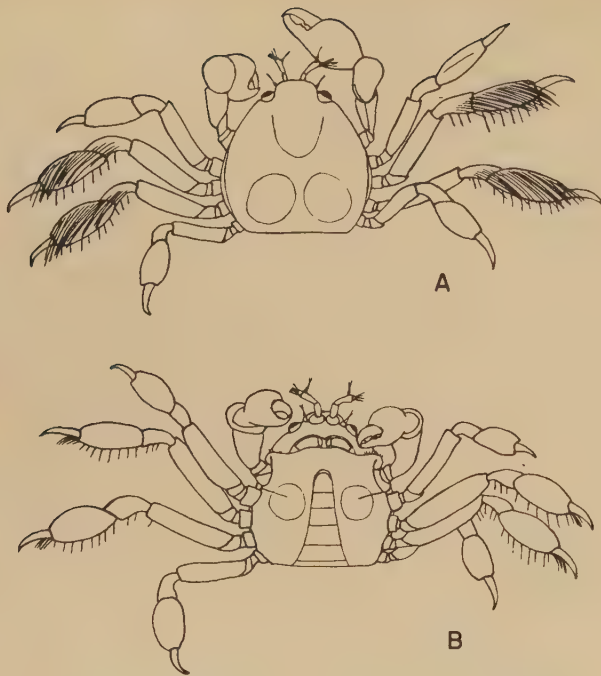


FIGURE 188.—*Pinnothereos ostreum* Say. A, stage I female in dorsal view; B, stage I female in ventral view; approximately $\times 9$ (after Stauber, 1945).

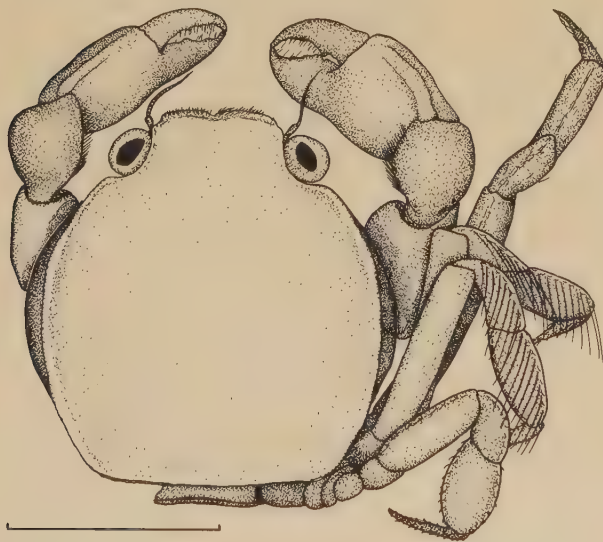


FIGURE 189.—*Pinnothereos ostreum* Say. Male in dorsal view, walking legs of left side not shown, 1 mm. indicated.

only. Outer maxilliped with ischium and merus fused; carpus, or first article, of palp short, oblong; propodus elongate, end rounded; dactyl inserted behind middle of propodus, minute, slender.

Chelipeds small; merus and carpus rather slender. Palm somewhat flattened inside, swollen outside, strongly widened from proximal toward distal end, then narrowed; width across base of fingers less than greatest width of palm; fingers, especially immovable one, stout, not gaping, tips hooked past each other, minute teeth on opposed edges, a larger tooth near base of each, immovable finger horizontal. Walking legs slender, subcylindrical; last two articles with thin fringe of hair; second and third legs about equal in length, first legs slightly stouter, last pair turned backward and upward.

Abdomen large, extending beyond carapace in all directions.

Measurements.—Carapace: width, ranging from 4 to 15 mm. (Christensen and McDermott, 1958).

Color.—Whitish or salmon pink.

Recognition characters.—Mature male and hard-stage female: Carapace well calcified, flat dorsally, subcircular in outline, with truncate front more advanced than in mature female. Posterior margin straight; lateral margin thin, rather sharply bent from dorsal side, margin marked by a raised band of short dense hair. Eyes well developed. Buccal mass crescentic, arched, broad from side to side but short anteroposteriorly; cavity completely closed by external maxillipeds formed as in mature female.

Chelipeds stout; merus and carpus not slender as in mature female. Palm slightly flattened inside, swollen outside, and shaped as in mature female, both margins convex. Hand with bands of pubescence on upper and outer surface of palm, and outer surface of immovable finger. Fingers stout, especially immovable finger, with tips hooked past each other when closed; dactyl with small tooth proximally, tooth fitting between two protuberances on immovable finger when closed; both fingers with stiff hairs on gripping edges. Walking legs flattened, with posterior margins thickened, and with plumose swimming hairs on second and third pairs.

Abdomen narrow, confined to sternal depression; copulatory stylets of male well developed, first pair bladeliike and hairy, second pair rodlike and almost hairless (Stauber, 1945).

Measurements.—Carapace: male, width, 1.4 to 4.6 mm.; female, width, 1.3 to 2.7 mm. (Christensen and McDermott, 1958).

Color.—Dark or medium-dark brown with two large, distinct, almost circular, pale white spots on both carapace and sternum; dorsal spots on branchial regions, ventral spots flanking abdomen and medial to first pair of legs; color and spots persistent in alcohol (various authors).

Habitat.—Parasitic [or commensal] chiefly in the oyster, *Crassostrea virginica*, also in *Pecten* spp. and *Anomia simplex* (Christensen and McDermott, 1958), and in *Mytilus edulis* (McDermott, 1961). Also occasionally found in *Chaetopterus* tubes (Gray, 1961).

Type locality.—Given as—"inhabiting the common oyster."

Known range.—Salem, Mass., to State of Santa Catarina, Brazil.

Remarks.—Say's *P. depressus* appears almost certainly to be the hard-stage male as described above and discussed below.

The works of Hyman (1924a), Stauber (1945), Sandoz and Hopkins (1947), and Christensen and McDermott (1958) together have made knowledge of the biology and life history of *P. ostreum* the most complete for any species of *Pinnotheres* in the world. The serious student should refer to these thorough works, for they can be summarized only in barest outline here. The complex life cycle of this species encompasses many developmental stages, as well as a striking sexual dimorphism in the mature animals, which, together with the structural specializations and mode of existence, demonstrate a beautiful accommodation to an unusual habitat.

The larval stages include four zoeae followed by one megalops. The first two zoeal stages were described by Hyman (1924a), and a description of all these stages (partial for fourth zoeal stage) was given by Sandoz and Hopkins (1947). In general, the zoeae and megalops have no dorsal or lateral spines on the carapace. Time of development from hatching to molting of the megalops to first crab stage is 25 days.

From the first crab stage on, development is summarized by Christensen and McDermott (1958, p. 154). The first crab stage, actually the stage which invades oysters, is called the invasive stage by these authors. It was described by Sandoz

and Hopkins (1947) and in many respects is similar to the later hard stage in its flattened shape, legs adapted for swimming, and characteristic color markings (carapace width, 0.59–0.73 mm.).

In Delaware Bay, few invasions take place before August 1. The peak of oyster setting there is in July; spat will have grown to size sufficient to harbor one or more crabs by the peak of the crab invasions in September. Though invasive stages in oysters are found all winter, growth and development stop about the first of November when water temperatures begin to drop below 15° C. Surprisingly small spat may be invaded. Two crabs were found in an oyster 4.2 mm. long, and in larger spat up to seven crabs were found in a single specimen. The crabs prefer to invade spat or yearling oysters rather than older ones (76.7, 54.6, and 21.5, being respective infestation percentages for a given year class of crabs), but survival rate of crabs is better in yearlings and older oysters.

Following the invasive stage are two ill-defined stages designated as prehard. These stages, described by Christensen and McDermott (1958), are soft and resemble later posthard stages of the females (carapace width: male, 1.4–4.6; female, 0.75–2.7 mm.). The legs are rounded and not adapted for swimming. These stages are found in all parts of the water-conducting system of infested oysters. In the region of Delaware Bay, most young crabs reach the prehard stages before growth ceases in fall and they overwinter in these stages. Development resumes when temperatures rise above 15° C.

The hard stage, formerly regarded as the invasive stage, is characterized above. On the average, males are larger than females, as they are in the preceding stages. The form of this stage resembles that of the invasive stage, and males of this stage swim freely. This is the copulatory stage, and the males normally die in this stage.

The succeeding female stages, described by Stauber (1945), resemble the adult female, and are found only in the host on the gills. Stage II (the hard stage was designated as stage I by Stauber) has a thin flexible carapace but a narrow abdomen contained wholly in the sternal groove (carapace width, 1.3–3.1 mm.). Stage III has an abdomen extending beyond the depression in the sternum (carapace width, 2.6–4.4 mm.). Stage IV

has a relatively wide abdomen reaching the coxae of the legs in most cases (carapace width, 3.6–8.9 mm.). Stage V is the adult female described above.

The posthard stages are passed through rapidly. In Delaware Bay by mid-July, 62 percent of females have developed from the overwintering stage to maturity. By mid-August, 95 percent are mature and more than half are ovigerous; thus, *P. ostreum* reaches maturity within its first year. Males live 1 year or less, but females continue to grow after they have hatched their first batch of eggs and may live to an age of 2 or 3 years, though many probably die after they have hatched their eggs in the second summer. In the second or third year, females may become ovigerous as early as mid-June, and ovigerous yearlings may occur as late as mid-October. Farther south the breeding season is more extended, and ovigerous females have been collected near Ocracoke, N.C., as early as mid-April.

Ovigerous females measuring 9.4 and 10.8 mm. in width carried 7,957 and 9,456 eggs respectively. It is not known how long a female carries eggs, but it is believed to be 3 to 5 weeks. The females produce only one batch of eggs the first year but in a second or third year may produce twice.

Except for the brief free-swimming periods in the invasive hard stages, the crabs lead a parasitic existence. Stauber (1945) and Christensen and McDermott (1958) both found that the crab feeds on food filtered from water by the host by picking food strings from the margins of the gills with its chelipeds. The crab also will catch newly formed mucus-food masses with its walking legs and then reach beneath the abdomen with its chelipeds, comb the legs, and pass the food on to the mouth. The method of feeding for young crabs not on the gills is unknown, but they may filter food with the mouth parts. Posthard stages are found only on the gills, indicating that feeding on the food-laden mucus alone can insure adequate food for rapid growth and egg production. Growth of females is positively correlated with size of host and is probably related to food supply and amount of water pumping by the host.

The ordinary feeding activities are harmful to the host (Stauber, 1945), particularly causing gill erosion of two types, local erosion of one or more demibranchs, and an extensive shortening of demi-

branches from the anterior end of gills to a point ventral to the adductor muscle. Christensen and McDermott (1958) noted that this erosion is a progressive process and nearly all infested oysters show some gill damage, some few older oysters having hardly any gill tissue left. Usually, however, only presence of a mature crab over a long time will noticeably affect growth of an oyster in normal environmental circumstances.

Pinnotheres maculatus Say. Mussel crab

Figure 190

Pinnotheres maculatus Say, 1818, p. 450.

Pinnotheres maculatus: Rathbun, 1918b, p. 74, text-figs. 35–36, pl. 17, figs. 3–6 (rev.).—Hay and Shore, 1918, p. 443, pl. 35, fig. 10.

Recognition characters.—Mature female: carapace suborbicular, somewhat broader than long, thick and firm but not hard, convex, smooth; surface uneven, covered with a short, dense, deciduous tomentum. Gastrocardiac area higher than, and separated by depressions from, branchiohepatic area. Front slightly advanced, approximately one-fifth width of carapace, subtruncate in dorsal view, slightly bilobed. Orbits small, subcircular, eyes spherical. Antenna longer than width of orbit; antennule large, obliquely transverse. Buccal mass roughly quadrangular, crescentic, much broader than long; ischium and merus of external maxilliped united; propodus larger than carpus; dactyl narrow, curved, spatulate, attached near middle of propodus, and reaching to near extremity of propodus.

Chelipeds moderately stout, articles subcylindrical and more or less pubescent; carpus elongate; palm thick, blunt edged, increasing in size distally; fingers stout, fitting closely together with tips hooking past each other; immovable finger nearly horizontal; dactyl with tooth near base fitting into sinus with tooth at either side on immovable finger. Walking legs slender, hairy above and below; second pair longest, shorter than chelipeds; first three dactyls falcate, shorter than propodi; last leg shortest, turned forward and upward, with long dactyl equaling propodus.

Abdomen large, extending to bases of legs.

Measurements.—Carapace: length, 13.7 mm.; width, 14.3 mm.

Color.—Obscure brown.

Recognition characters.—Mature male: Carapace flat, subcircular, diameter about half as great



FIGURE 190.—*Pinnotheres maculatus* Say. Upper drawing: male in dorsal view, 2 mm. indicated; Lower drawing: female in dorsal view, 3 mm. indicated.

as female, somewhat longer than wide, harder than female. Regions superficially defined more by color than by structural prominence, light areas mostly elevated, usually allowing pubescence to wear; gastric, cardiac, and branchial regions separated by broad, shallow, confluent indentations. Front broad, prominent, depressed, slightly bilobed, approximately one-third width of carapace. Orbits subcircular, eyes large. Antennae somewhat longer than width of orbit.

Chelipeds shorter than in female, hands stouter. Walking legs wider, especially propodal articles of first three legs; posterior surface overlaid with thin fringe of hairs attached near upper margin; last leg relatively shorter than in female, not reaching propodus of third, dactyl more nearly like third than in female.

Abdomen at middle approximately one-third width of sternum, gradually narrowing from

third to seventh segment, sides of third convex, of seventh obtusely rounded; sutures between segments of abdomen and sternum with narrow lines of dark pubescence.

Measurements.—Carapace: length, 9.1 mm.; width, 8.7 mm.

Color.—Striking light dorsal color pattern of bare spots on a background of dark pubescence consisting of a median stripe constricted in middle and behind, a subtriangular spot on each side in front of middle, and a linear spot on each side behind. Chelipeds with dark pubescence on inner and upper surface of carpus, a bit on upper surface of merus and inner side of palm proximally, otherwise scattered flecks on hands and walking legs.

Variations.—Young females resemble dark-colored males except in shape of the abdomen and the character of its appendages. Such females are free swimming and range upward in length to 5.2 mm. More mature females, light colored and commensal or parasitic in habit, range from 3.3 mm. in length upward. In such small and medium sized females the long hair on the legs persists.

Some males resemble mature females in coloration and structure of legs, ranging in length from about 4 mm. upward. Such males are commensal or parasitic in habit.

Individuals vary in stoutness of chelae, and in length and curvature of dactyls on the second legs. Normally this dactyl is like the dactyls on the first and third legs, but may be straightened and longer, and may occur on one or both sides of an individual and in different individuals in the same lot.

Habitat.—Mature males and females are commensal or parasitic in *Mytilus edulis*, *Modiolus modiolus*, *M. americanus*, *Mya arenaria*, *Aequipecten gibbus*, *A. irradians*, *Placopecten magellanicus*, oyster (?), *Atrina serrata*, and in tubes of *Chaetopterus variopedatus*, from *Molgula robusta*, the pharynx of *Bostrichobranchus pilularis*, and on *Asterias vulgaris*. The free-swimming stages have been found in bays and sounds. Surface to 25 fathoms.

Type locality.—Given as—"inhabits the muricated *Pinna* of our coast."

Known range.—Off Marthas Vineyard, Mass., to Mar del Plata, Argentina.

Remarks.—Though no detailed life-history studies have been made on this species comparable

to those on *P. ostreum*, more incidental data are available on mature individuals of both sexes from casual collecting. Ovigerous females have been found through most of the range of distribution. They have been reported in January from St. Thomas, March from Jamaica, May to November from Florida, June to January from North Carolina, July to September from Massachusetts and Rhode Island, and in June in Brazil (Rathbun, 1918b, and U.S. National Museum records). Hyman (1924a) described the first stage zoea which, unlike the zoeae of *P. ostreum*, has well-developed spines on the carapace. These zoeae are common near Beaufort, N.C., throughout the summer.

As in *P. ostreum*, the hard stage is found in both males and females and, though both swim actively, the males predominate in open water. An invasive stage may precede the relatively large hard stage as in *P. ostreum*. Unlike *P. ostreum* males, at least some *P. maculatus* males apparently live beyond the hard stage, for larger, somewhat globose males, resembling females in adaptation to parasitic or commensal life, occur in some hosts (see variations above).

Welsh (1932) found the swimming velocity of *P. maculatus* larvae to be greatly influenced by temperature and light intensity. The larvae are sensitive to only a small range of light intensity. At temperatures between 20° and 25° C. the maximum velocity of swimming is attained at intensities between 10 and 25 meter-candles. When series of measurements are made to determine the effective light at different constant temperatures, it is found that, besides a marked effect on general activity, there is a change in the relationship of velocity to intensity; slopes of curves showing these relationships change, and the maximum possible velocity of swimming for each temperature is reached earlier at the higher temperatures.

Genus *Parapinnixa* Holmes, 1894

Rathbun, 1918b, p. 107.

Parapinnixa bouvieri Rathbun

Figure 191

Parapinnixa bouvieri Rathbun, 1918b, p. 111, text-fig. 60, pl. 25, figs. 4-10.

Recognition characters.—Minute. Carapace smooth, shining, not more than twice as wide as long, longitudinally very convex, slightly convex

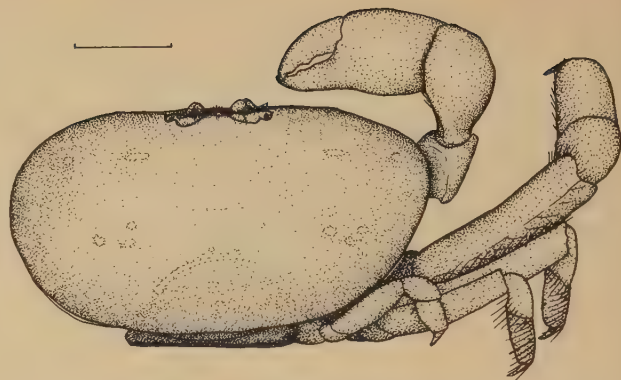


FIGURE 191.—*Parapinnixa bouvieri* Rathbun. Ovigerous female in dorsal view, legs of left side not shown, 1 mm. indicated.

transversely, sides arcuate; widest part with a thin pubescent margin on lower edge; anterior margin nearly straight, a row of four distant pits behind margin. Frontoorbital width about one-third carapace width. Front broadly triangular, deflexed, tip invisible in dorsal view, edge emarginate and pubescent; a pubescent groove running parallel to and immediately behind front terminating in orbital margins. Orbits circular, filled by eyes, cornea black, visible from above. Antennular cavities large, not wholly separated from each other or from orbits, and extending laterally beyond minute antennae. Outer maxilliped triangular when folded in place, two free corners rounded, longitudinal side approximately two-thirds as long as posterior side; ischium and merus fused, obliquely truncate distally leaving first joint of palp exposed; propodus elongate, distally tapering; dactyl small, suboval, both articles folding under merus.

Chelipeds short, stout, merus especially, partly hairy inside; palms thick, hairy outside; lower margin convex; immovable finger subtriangular, broad at base, a small tooth on gripping edge near tip; dactyl with small basal tooth, remainder of edge finely and irregularly denticulate. Walking legs with edges more or less pubescent, second and third pairs with line of long hairs applied to posterior surface of carpus and propodus; first leg thick, merus not reaching laterally beyond carpus of cheliped; second and third leg about equal; fourth small, not exceeding merus of third; dactyls of second and third legs longer and more slender than of first and fourth.

Male abdomen with sides gradually convergent, seventh segment not more than 1.5 times as long as wide; female abdomen with sides of triangular portion straight.

Measurements.—Carapace: female, length, 1.6 mm., width, 3.1 mm.; male, length, 2 mm., width, 3.5 mm.

Habitat.—Approximately 3 or 4 to 40 fathoms.

Type locality.—Off Cape Catoche, Yucatan, [Mexico]; *Albatross* station 2362.

Known range.—Off Charleston, S.C.; south of Tortugas, Fla.; Puerto Rico; and type locality.

Remarks.—Ovigerous females have been taken in Florida in August. The ovigerous specimen taken in Puerto Rico (no date) was found among ventral spines of a rose sea urchin (J. A. Rivero, U.S. National Museum).

Genus *Dissodactylus* Smith, 1870

Rathbun, 1918b, p. 114.—Hemming, 1958b, p. 31.

Dissodactylus mellitae Rathbun

Figure 192

Echinophilis mellitae Rathbun, 1900a, p. 590.

Dissodactylus mellitae: Rathbun, 1918b, p. 117, text-fig. 66, pl. 28, figs. 7–8 (rev.).—Hay and Shore, 1918, p. 444, pl. 36, fig. 1.

Recognition characters.—Minute. Carapace about one-fourth wider than long, slightly wider at lateral angles than posteriorly, dorsal surface convex, smooth, and polished except anterior portions slightly pubescent. Edge of front concave, fringed with short hairs. Anterolateral borders arcuate, with a fine raised rim curving inward on carapace at lateral angles and continuing medio-posteriorly for some distance; posterior margin sinuous. Orbits opening medially, eyes small.

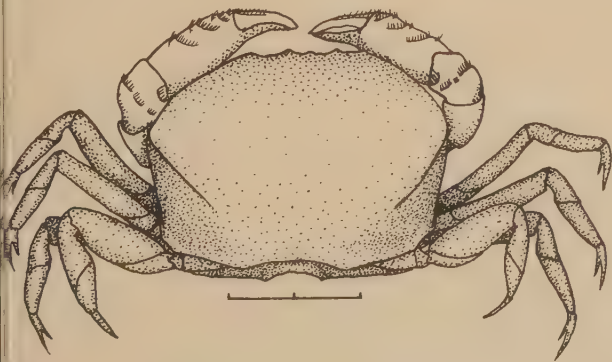


FIGURE 192.—*Dissodactylus mellitae* Rathbun. Animal in dorsal view, 2 mm. indicated.

Outer maxilliped with fused, spatulate merus and ischium; outer edge of carpus arcuate; propodus quadrate.

Chelipeds short and stout; hand longer than other articles combined, cylindrical, upper and outer faces bearing a few impressed, short, oblique lines with short appressed hairs extending distally; fingers considerably shorter than palm, bent inward and curved, opposable margins with tufts of short bristles; carpus with a distal fringe of short hairs and an impressed line similar to those on chelae; merus short and stout, lower surface with oblique lines. First, second, and third walking legs stout, margins fringed with short hairs, dactyls deeply bifid; fourth walking legs with styliform dactyls, fringed with long hairs on margins.

Abdomen of male with first and second, and third to fifth segments partially fused, margins convex; telson subtriangular with convex sides. Abdomen of female with first segment linear, second to fourth fused; telson broadly triangular, half as wide as sixth segment, sides sinuous.

Measurements.—Carapace: male, length, 2.9 mm., width, 3.5 mm.; ovigerous female, length, 3.3 mm., width, 4.5 mm.

Color.—Light, with scanty dark mottlings which persist in alcohol and are then of purplish color (Rathbun, 1918b).

Habitat.—This species clings to the outside of the keyhole urchin *Mellita quinquesperforata* and the sand dollars *Echinarachnius parma* and *Encope michelini*. The crabs are easily overlooked because as the sand dollars are lifted from the water, the small crabs may move about and drop off. Shallow water to 11.5 fathoms.

Type locality.—Pensacola, Fla., on *Mellita quinquesperforata*.

Known range.—Western part of Vineyard Sound, Mass., to Charleston, S.C.; western Florida.

Remarks.—Hyman (1924a) described the first zoeal stage of this crab, comparing it to the zoea of *Pinnotheres maculatus*, and reported it as common in plankton tows in the Beaufort, N.C., area in summer. Ovigerous females occur there during the same period, and are reported from Narragansett Bay in August (Rathbun, 1918b), and in Florida from July to October (Wass, 1955, in part).

Subfamily Pinnothereliinae

Carapace transverse, usually broadly so. Ischium of external maxilliped usually distinct from merus, though smaller and sometimes imperfectly united with it. Merus longitudinal or somewhat oblique; palp of good size, sometimes as large as merus-ischium (Rathbun, 1918b).

Genus *Pinnixa* White, 1846

Rathbun, 1918b, p. 128.—Hemming, 1958b, p. 35.

KEY TO SPECIES IN THE CAROLINAS

- a. Posterior part of carapace with conspicuous, sharp, transverse ridge extending uninterruptedly from side to side.....*cristata* (p. 210).
- aa. Posterior part of carapace without ridge, or with ridge on cardiac region only.
 - b. Chela with immovable finger bent downward.
 - c. Propodus of third walking leg less than twice as long as wide.....*chaetoptera* (p. 210).
 - cc. Propodus of third walking leg slender, twice or more than twice as long as wide.....*sayana* (p. 212).
 - bb. Chela with immovable finger straight or nearly so, not bent downward.
 - c. No cardiac ridge present.....*retinens* (p. 212).
 - cc. With cardiac ridge present.
 - d. Merus of third walking leg with posterior surface not deeply cupped out.....*cylindrica* (p. 213).
 - dd. Merus of third walking leg with posterior surface deeply cupped out.....*lunzi* (p. 214).

Pinnixa cristata Rathbun

Figure 193

Pinnixa cristata Rathbun, 1900a, p. 589.—1918b, p. 134, text-fig. 78, pl. 29, figs. 8-9 (rev.).—Hay and Shore, 1918, p. 446, pl. 36, fig. 5.

Recognition characters.—Carapace short, surface punctate, wrinkled, and microscopically granulate, slightly pubescent at extreme outer corners; a high, sharp, almost straight ridge extending without a break entirely across cara-

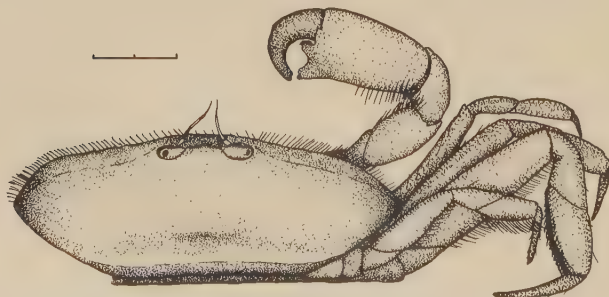


FIGURE 193.—*Pinnixa cristata* Rathbun. Male in dorsal view, legs of left side not shown, 2 mm. indicated.

pace somewhat in front of posterior border; a deep furrow behind gastric region. Anterolateral margin with a raised crest stopping short of hepatic region; posterior margin wide, concave. Front deflexed, not advanced. Orbit no wider than half of front.

Chelipeds rather stout; palm oblong with upper and lower margins convex, surface covered with reticulate pattern of fine granulations; immovable finger short, deflexed, gripping edge with a truncate subbasal tooth, another small tooth distally forming a truncate tip; dactyl long, gaping, with inner margin bent in a curved right angle. Walking legs somewhat longer than in related species, sparsely hairy along margins only, third walking leg strongest; dactyls slender, slightly curved on first three, straight on last walking leg.

Measurements.—Carapace: female, length, 4 mm.; width, 11 mm.

Type locality.—Beaufort, N.C.

Known range.—Beaufort, N.C., to Edisto Island, S.C.; Grand Isle, La., to Long Lake, Black-jack Peninsula, Aransas County, Tex. (Hedgpeth, 1950, and U.S. National Museum records).

Remarks.—The species has been taken from sandy beaches by digging or sifting in North Carolina and South Carolina, and Louisiana, and from the mouth of *Galeichthys felis* in Louisiana.

Pinnixa chaetoptera Stimpson

Figure 194

Pinnixa chaetoptera Stimpson, 1860a, p. 235.—Rathbun, 1918b, p. 151, text-figs. 93-94, pl. 33, figs. 3-6 (rev.).—Hay and Shore, 1918, p. 445, pl. 36, fig. 4.

Recognition characters.—Carapace transversely oval, somewhat more than twice as wide as long, more swollen in female than in male, surface uneven, sides densely pubescent. Regions well defined by pubescent grooves; cardiac region with an acute transverse crest broadly interrupted in middle forming two dentiform prominences, more conspicuous in male than in female; subbranchial region advanced, forming a prominent shoulder with granulated edge. Posterior margin concave. Front narrow, with a deep median groove.

Chelipeds stout, smooth, pubescent. Hand in male with distal palmar edge perpendicular; immovable finger short, deflected, truncate at tip, with a prominent rounded tooth on cutting edge; dactyl strongly curved, almost vertical, forming

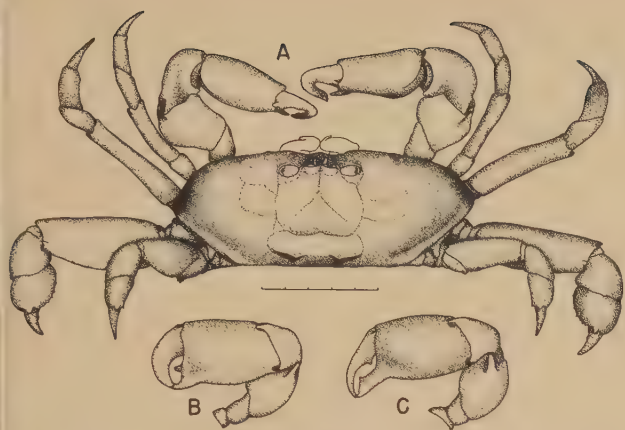


FIGURE 194.—*Pinnixa chaetopterana* Stimpson. A, male in dorsal view; B, chela of male in frontal view; C, chela of female in frontal view; 5 mm. indicated.

oval gape when closed with tips of fingers meeting. Hand of female relatively smaller; immovable finger with tooth somewhat beyond middle followed by an irregularly dentate, raised, cutting edge terminating in a blunt tip; dactyl with a small basal tooth, longer than in male, fingers agape proximal to cutting portion when closed with tips crossing each other. First and second pairs of walking legs slender, propodi with distal V-shaped row of spinules on lower border; dactyls with one or more short rows of spinules. Third pair longer and much stouter, conspicuously pubescent, and with inferoposterior margins of ischium, merus, and propodus dentate; fourth pair like third but smaller, with minute spinules on dactyls.

Male abdomen with sixth segment slightly constricted laterally at middle; telson semicircular.

Measurements.—Carapace: male, length, 6 mm., width, 14 mm.; female, length, 6 mm., width, 11 mm.

Variations.—Wass (1955) pointed out that two forms of this species occur on the northern Gulf of Mexico coast, a larger and smaller form.

Color.—Nearly white, but usually much obscured by brown or blackish hairs and by dirt collected in them; eggs bluish (various authors).

Habitat.—The large form of this crab lives commensally with the worms *Chaetopterus variopedatus* and *Amphitrite ornata*, and is seldom found outside their tubes. The small form lives in the upper portion of *Callianassa* burrows on the

northern Gulf coast (Wass, 1955). Intertidal to 8.5 fathoms.

Type locality.—Charleston Harbor, S.C., on muddy or clayey shores in tubes of *Chaetopterus variopedatus* [= *pergamentaceus*].

Known range.—Wellfleet, Mass., to South Carolina; Punta Rassa, Fla., to Galveston, Tex.; Rio de Janeiro, and Villa Bella, São Sebastião, Brazil.

Remarks.—Ovigerous females have been reported from Beaufort, N.C., between April (Gray, 1961) and late October (Enders, 1905), from Florida in October (Wass, 1955) and February (Gray, 1961), and from southern Massachusetts in July and August (Pearse, 1913; Rathbun, 1918b). Otherwise they are known from South Carolina in February. Faxon (1879) and Hyman (1924a) described the first zoeal stage.

Some habits of this crab were observed by Pearse (1913) at Woods Hole, Mass. The species is strongly thigmotactic. Crabs placed on sand in an aquarium usually buried themselves, but soon explored the surface and entered and remained in glass tubes left lying on the sand. In experiments, crabs found a buried, artificial "*Chaetopterus* tube" by accident. Adult crabs could enter or leave this tube. The crabs moved either forward or sideways on sand. The third walking leg was the chief locomotor organ, but in tubes the crabs braced themselves with all the legs.

Crabs placed in standing water in an artificial worm tube were able to exist for 8 days before leaving the tube for better aerated water. The crabs' respiratory currents were feeble and inconstant in direction and force. Crabs were usually fouled with encrusting organisms and they took no trouble to clean their bodies except for mouth parts, eyes, and antennae. They fed by extending the fringed external maxillipeds and sweeping them toward the mouth, filtering small particles from the water, then cleaning the fringe with other mouth parts.

Gray (1961, see also account for *Polyonyx gibbesi*) described *Pinnixa chaetopterana* as primarily a mud crab and a facultative commensal of *Chaetopterus*. He found that the crabs readily enter and leave the tubes of the host, and if diameter of the parchment chimney of the worm tube is too small, the crab bites a hole at the base of the chimney to make an entrance or exit.

Figure 195

Pinnixa sayana Stimpson, 1860a, p. 236; Rathbun, 1918b, p. 156, text-fig. 98, pl. 34, figs. 2-4 (rev.).—Hay and Shore, 1918, p. 446, pl. 36, fig. 3.

Recognition characters.—Carapace smooth, polished, lightly pubescent on sides, depressed at middle, a low, ill-defined, transverse ridge parallel with and close to posterior margin extending about one-third width of carapace. Anterolateral slope with similar ridge, lateral two-thirds of crest beaded. Front deeply grooved above.

Chelipeds with hands stout, compressed, hardly twice as long as broad; immovable finger very short, with truncate basal tooth; dactyl strongly curved. Walking legs long and slender, smooth; first walking leg reaching to propodus of second; second and third leg same length; fourth reaching beyond middle of carpus of third; merus of third leg approximately 3.5 times as long as wide, lower margin, and that of propodus, minutely denticulate; dactyls of first two legs slightly curved, of third straight, posterior edge of last dactyl slightly convex.

Measurements.—Carapace: male, length, 5 mm., width, 10 mm.; female, length, 4 mm., width, 7 mm.

Variations.—Females differ from males in that the cardiac ridge is lower and less sharp, the fingers do not gape, the immovable finger is longer and less bent, and the dactyl on the chela is more oblique.

Color.—Almost white, but lightly stained with brown.

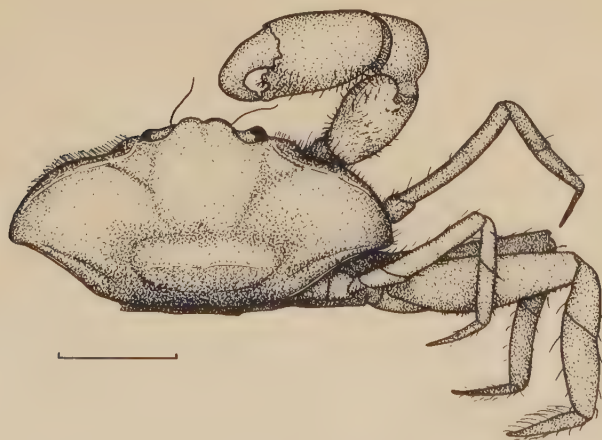


FIGURE 195.—*Pinnixa sayana* Stimpson. Male in dorsal view, legs of left side not shown, 1 mm. indicated.

Habitat.—The species has been found free in the water, has been dug out of mud, and is said to be found in the tubes of *Arenicola cristata*; shore to 26 fathoms.

Type locality.—Mouth of Beaufort Harbor, N.C., 6 fathoms, sandy mud.

Known range.—Vineyard Sound, Mass., to Beaufort, N.C.; Sarasota Bay, Fla., to Grand Isle, La.

Remarks.—Ovigerous females have been reported in August from Narragansett Bay, R.I. (Rathbun, 1918b), and are known in September from Louisiana. The last zoeal stage of a *Pinnixa*, commonly found off the New England coast and described by Faxon (1879), was tentatively referred to this species by Smith (1880a). Both Faxon and Smith found the first crab stage to follow immediately the last zoeal stage. These stages in development of *P. sayana* were summarized and illustrated by Hyman (1924a).

Pinnixa retinens Rathbun

Figure 196

Pinnixa retinens Rathbun, 1918b, p. 139, text-figs. 83-84, pl. 41, figs. 1-2.

Recognition characters.—Carapace nearly twice as wide as long, almost flat, except sloping downward toward margins; regions indicated. Lateral margin marked by sharp, granulate ridge reaching to subhepatic sulcus, no cardiac ridge; posterior margin preceded by a subparallel groove. Outer maxilliped with obliquely spatuliform dactyl attached to middle of inner margin of propodus.

Chelipeds small, approximately as long as first leg; hand with lower margin straight, suboblong, marginate below; fingers slender, subequal, not gaping; dactyl with tooth at proximal third of gripping edge. First and second walking legs similar; second a little longer, dactyls slightly curved, long, pointed. Third walking leg stout, exceeding second by length of dactyl and half of propodus; lower edge of ischium, merus, and propodus armed with stout spinules; posterodistal end of ischium prolonged in a stout, curved spine with point directed upward and backward; dactyl more curved than in first and second legs, pointed. Last leg extending to distal end of third merus; dactyl stout, nearly straight, tip curved slightly upward.

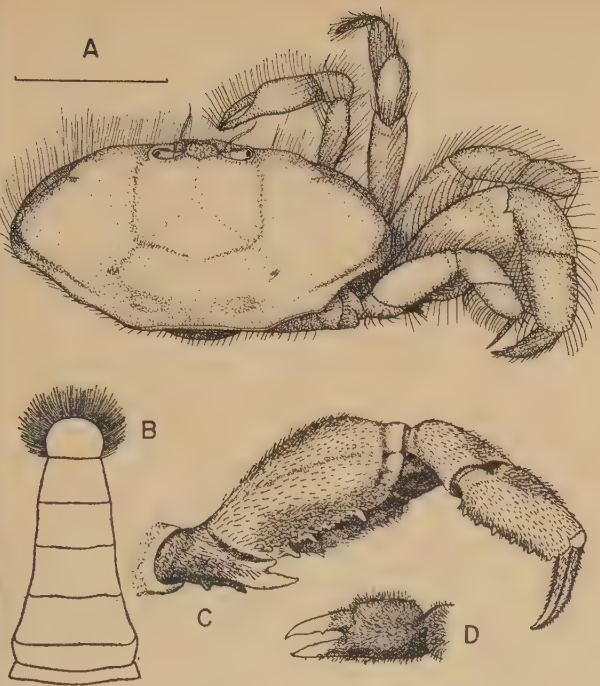


FIGURE 196.—*Pinnixa retinens* Rathbun. A, female in dorsal view, legs of left side not shown, 5 mm. indicated; B, male abdomen; C, male third walking leg, lower side; D, male left chela; B-D, holotype approximately $\times 9$ (after Rathbun, 1918b).

Abdomen constricted at base of second segment, widest between second and third, and tapering to base of telson; telson wider than long; anterior and posterior margins of sternal segments granulate.

Measurements.—Carapace: male, length, 4 mm., width, 7 mm.; ovigerous female, length, 6 mm., width, 12 mm.

Habitat.—An ovigerous female was taken from the burrow of *Upogebia affinis* at Alligator Harbor, Fla., in June (Wass, 1955). Small specimens have recently been taken from mud bottom in Chesapeake Bay (Wass, personal communication). Near low-tide mark to 20 fathoms.

Type locality.—Chesapeake Bay, off Poplar Island, Md., 20 fathoms, soft bottom.

Known range.—Chesapeake Bay; Alligator Harbor, Fla.; Aransas area of Texas coast (U.S. National Museum records).

Remarks.—Though this species has never been reported in the Carolinas, its occurrence in the above localities would indicate that it probably ranges at least between them.

Pinnixa cylindrica (Say)

Figure 197

Pinnotheres cylindricum Say, 1818, p. 452.

Pinnixa cylindrica: Rathbun, 1918b, p. 159, text-fig. 99, pl. 35, figs. 5, 8 (rev.).—Hay and Shore, 1918, p. 446, pl. 36, fig. 2.

Recognition characters.—Carapace smooth, polished, punctate, punctations small and scarce in middle third, large and more numerous elsewhere; pubescent at extreme outer corners; depressed in middle; anterior cardiac region separated from gastric and branchial regions by a groove. Anterolateral portions with a sharp granulate crest not reaching cervical suture; middle of cardiac region crossed by a transverse (sometimes inconspicuous) ridge; posterior border short, somewhat concave. Front not prominent, bilobed, with submarginal groove.

Chelipeds moderately stout, smooth, punctate; hands suboval, approximately 1.5 times as long as wide; fingers horizontal, subequal in length, tips strongly hooked, overlapping when closed, leaving a gape; immovable finger with tooth near tip; dactyl with a tooth near middle; a finely milled crest running from tip of immovable finger backward and upward approximately two-fifths length of palm on outer surface. First walking leg slender, reaching to propodus of second; second stouter, reaching to middle of dactyl of third; third leg stoutest, merus 1.6 times as long as wide, distally narrowed, upper and lower margins finely granulate; fourth short; dactyls nearly straight, that of fourth leg convex posteriorly, slightly concave anteriorly.

Abdomen of male with sixth segment constricted laterally, constriction narrower than telson.

Measurements.—Carapace: male, length, 7 mm., width, 14 mm.; female, length, 10 mm., width, 20 mm. (McDermott, 1962).

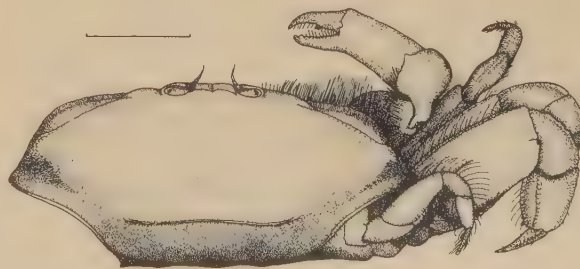


FIGURE 197.—*Pinnixa cylindrica* (Say). Female in dorsal view, legs of left side not shown, 5 mm. indicated.

Color.—Yellowish gray, light to dark brown, or sometimes grayish, and mottled with dark gray and/or white. Rhythmic chromatophore changes as well as genetic differences may control observed variations (McDermott, 1962).

Habitat.—The species lives in burrows of *Arenicola cristata* Stimpson (Wass, 1955; McDermott, 1962), and possibly with other large annelids; shallow water to 20 fathoms.

Type locality.—Jekyll Island, Ga.

Known range.—North Falmouth, Mass., to Alligator Harbor, Fla.

Remarks.—McDermott (1962) summarized existing knowledge of the habits of this species and added numerous ecological observations. He reported the crab for the first time from New Jersey, finding it associated with 76 percent of the lugworms collected during summer. Crabs and worms were collected by manual digging. With one exception, single crabs were found on worms.

Of 18 female crabs found in July, 16 were ovigerous. One captive female produced eggs on July 7 and liberated zoeae "around" August 5. Crabs which liberated zoeae when collected produced new sponges of eggs which were in late stages of development approximately 30 days later. McDermott judged that this species produces at least two egg masses in a breeding season. Molting between broods did not occur in the laboratory.

Associates of *P. cylindrica* were found to be *Zoothamnium* sp., attached *Crepidula convexa* Say, and colonies of *Triticella elongata* (Osburn).

Pinnixa lunzi Glassell

Figures 198–199

Pinnixa lunzi Glassell, 1937, p. 3, figs. 1–8.

Recognition characters.—Carapace slightly more than twice as wide as long, punctate, regions indicated, borders flanged, with a shoulder formed near wide lateral angle. Gastric and cardiac regions separated by a depression connecting with a deeper depression on each side of these regions; a prominent cardiac ridge extending transversely almost across carapace with an abrupt slope from crest of ridge to posterior border. Front prominent, bilobed, truncate, upturned over antennules.

Chelipeds stout; hands of male shorter and stouter than in female, appearing disproportionately small in female; palm with margins subparallel in female, widest at base of dactyl in male; in both sexes fingers gaping; immovable finger horizontal, armed with row of small teeth, distal tooth largest; dactyl stout, curved, armed with median lobe. Walking legs stout. First two lightly crested with setae on merus; carpus crested with a sharp beaded rim; propodus armed with a row of fine, sharp, brown spinules; dactyls constricted, sharp pointed, fluted, with rows of small,

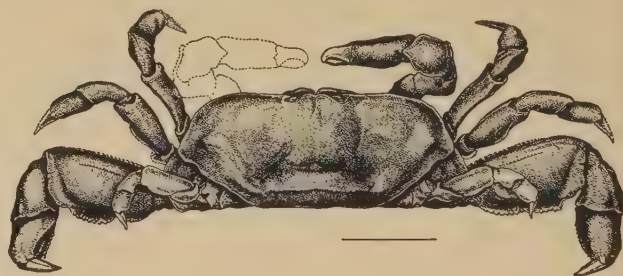


FIGURE 198.—*Pinnixa lunzi* Glassell. Male holotype in dorsal view, 7 mm. indicated (after Glassell, 1937).

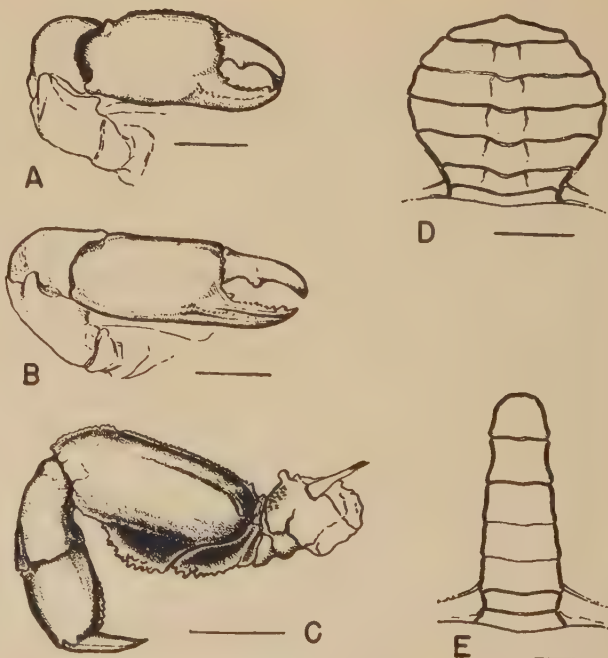


FIGURE 199.—*Pinnixa lunzi* Glassell. A, right chela of male; B, right chela of female, 3 mm. indicated; C, left third walking leg of female, 4 mm. indicated; D, abdomen of female, 6 mm. indicated; E, abdomen of male, 3 mm. indicated (after Glassell, 1937).

sharp, forward pointing spinules on crests. Third leg large; merus with two separated, upper, crenulated margins, lower border tuberculate, posterior surface with a deep, pubescent concavity, smooth within; ischium at lower distal end extending well past base of merus and with meral concavity continued on posterior face, lower border tuberculate; carpus and propodus together equal in length to upper length of merus; dactyl stout, nearly straight, without minute spinules. Fourth leg similar to third but smaller, merus with lower border tuberculate, dactyl slightly upturned at tip.

Male abdomen with telson semioval, sides not wider than concave sided sixth segment; third, fourth, and fifth segments partially fused.

Measurements.—Carapace: male, length, 9 mm., width, 21 mm.; female, length, 9 mm., width, 21 mm.

Color.—In alcohol, a muddy bluish brown; legs, abdomen, and chelipeds ivory.

Type locality.—Isle of Palms (about 15 miles northeast of Charleston, S.C.), washed on beach, under drift material.

Remarks.—The above account is taken chiefly from Glassell (1937). The types are the only known specimens and the host and habitat are unknown.

Family *Palicidae*

Carapace broadly transverse, subquadrilateral. Anterolateral margins dentate. Frontoorbital width great, front dentate. Orbits and eyes large. Buccal cavity quadrate, outer maxillipeds not covering it; ischium of third maxillipeds strongly produced forward on inner side; merus small, subtriangular, with a notch on inner distal side for articulation of palp. Afferent channels to branchiae opening at bases of chelipeds; efferent channels at anteroexternal angles of buccal cavity.

Chelipeds of moderate size, often unequal in male, usually tuberculate or granulate. Next three pairs of legs long, slender, and rough; last pair either very short and slender, subdorsal, smooth, or similar in position and ornamentation to other legs, and near size of first walking leg. Abdomen of male much narrower than sternum (Rathbun, 1918b).

Genus *Palicus* Phillipi, 1838

Rathbun, 1918b, p. 183; Holthuis and Gottleib, 1958, p. 104.

KEY TO SPECIES IN THE CAROLINAS

- a. Merus of second and third walking legs with an obtuse lobe at superodistal angle; frontal notch shallow, forming nearly a right angle at base-----*alternatus* (p. 215).
- aa. Merus of second and third walking legs with a prominent, sharp pointed lobe at superodistal angle; frontal notch deeper than wide-----*faxonii* (p. 216).

Palicus alternatus Rathbun

Figure 200

Palicus alternatus Rathbun, 1897a, p. 95.

Cymopolia alternata: Rathbun, 1918b, p. 188, text-fig. 117, pls. 42-43 (rev.).

Recognition characters.—Carapace broader than long, somewhat depressed, elevations covered with small tubercles composed of single or a few granules. Front broadly triangular, notched at middle, with four lobes or teeth, outer teeth less advanced than inner and broadly rounded. Eyes large; orbits deep, with upper border cut into teeth; middle tooth broad, obliquely truncate, bounded on each side by a V-shaped fissure; next tooth separated from outer tooth by a shallow sinus; outer tooth directed forward or a little outward, tip curved inward. First two anterolateral teeth dentiform with rounded tips, separated

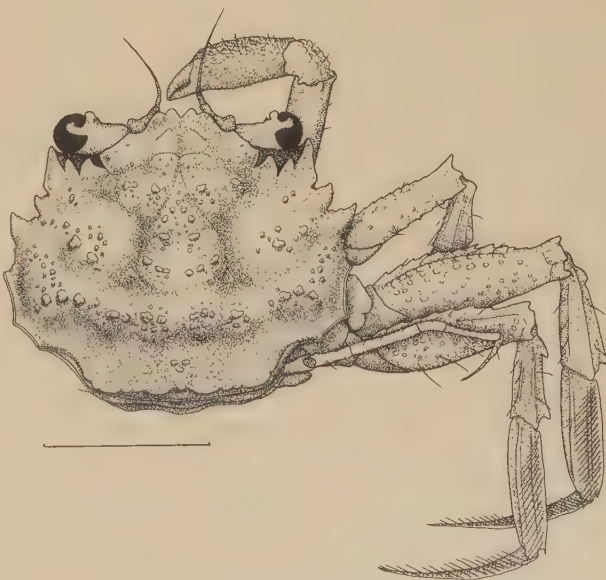


FIGURE 200.—*Palicus alternatus* Rathbun. Animal in dorsal view, legs of left side not shown, 5 mm. indicated.

by small V-shaped sinuses; third tooth rudimentary or in form of a small tubercle. Suborbital margin oblique, with two clefts; outer lobe nearly straight; inner lobe divided into two parts with inner angle produced in an acute tooth beyond triangular, pterygostomian lobe. Posterior margin bordered above by a thin, sinuous, elevated ridge broken into a variable number of unequal transverse tubercles with usually some granules interspersed.

Chelipeds of male occurring in two forms. In one form, chelipeds very unequal; on right side large and heavy, on left, slender and weak, both tuberculate and pubescent; carpus with an outer, laminated, lobed crest; hand surmounted by a similar double crest. Right hand very thick, width at distal end often equaling one-half length of carapace; immovable finger short, wide; dactyl strongly bent down, overlapping opposed finger and leaving a narrow gape. Left hand somewhat over one-third width of right, fingers long and narrow. In second, weaker form males, right hand about twice depth of left; fingers long and slender. Females with chelipeds more nearly equal.

Second pair of walking legs longer than others. First walking legs reaching middle of propodus of second, with posterior margin of propodus and proximal half of dactyl hairy in male; third walking leg reaching middle of dactyl of second, fourth leg slender, much shorter than third. Meri rough with squamous tubercles; with a single longitudinal groove on anterior surface, two on upper surface; first three meri with a superodistal lobe, subtriangular on first, subrectangular in second and third, lobe exceeding article in first, equal to article in second, not reaching end of article in third. Carpus with a rounded, anterior proximal lobe; anterior subdistal lobe low and rounded on first leg, triangular on second and third legs. Propodus with anterior margin convex, posterior margin straight.

Abdominal appendages of first form of male stout and twisted, tip bilobed, inner lobe thinner and longer than outer; second form of male with appendages weaker, not twisted, and tip less spreading.

Measurements.—Carapace: male, 7 mm., width, 8 mm.; female, length, 8 mm., width, 9 mm.

Variations.—This species shows great variation in structure. In some individuals the cara-

pace is wider behind in proportion to its length than in typical individuals, and the sides are less parallel. There is no consistency in relative size of the anterolateral teeth, for in some the first are largest and all teeth point forward, but in others the second teeth are largest and point slightly outward. In some individuals the anterodistal tooth on the merus of the second and third legs is more produced than in typical specimens, and there is variation in the length-width proportions of the propodus of the second leg. Details of lobulation on the front and lower margin of the eye are also subject to variation.

Habitat.—The species has been taken from a variety of fine and coarse bottoms (Rathbun, 1918b); 4 to 60 fathoms.

Type locality.—Lat. 29°11'30" N., long. 85°29'00" W., 26 fathoms (south of Cape San Blas, Fla.).

Known range.—Cape Hatteras, N.C.; Gulf of Mexico along west coast of Florida from Cape San Blas to Key West.

Remarks.—Ovigerous females have been reported in Florida from January to August, and from North Carolina in October (Rathbun, 1918b, and U.S. National Museum records).

Palicus faxoni Rathbun

Figure 201

Palicus faxoni Rathbun, 1897a, p. 96.

Cymopolia faxoni: Rathbun, 1918b, p. 194, text-fig. 120, pl. 45, figs. 2-3 (rev.).

Recognition characters.—Carapace broader than long, sides converging anteriorly; adult female quite convex, surface hairy, and with numerous tubercles and granules. Front broadly triangular; four frontal lobes well marked, outer pair not much wider than inner, median emargination deeper than wide with end often rounded, lateral emarginations shallow. Eyes large; orbits deep, with upper border cut into teeth by V-shaped sinuses, middle and outer teeth triangular, subacute, middle one equilateral, outer one narrow and separated from outer orbital tooth by a shallower sinus; outer tooth directed forward, tip oblique, its lateral margin nearly straight. Lateral border with two similar, sharp-pointed teeth, second one smaller, outer borders convex, inner concave. Lower margin of orbit oblique, bilobed; inner lobe in advance of outer, divided in two, outer portion rounded, inner portion a small acute



FIGURE 201.—*Palicus faxoni* (Rathbun). Male in dorsal view, legs of left side not shown; cheliped, second and third walking legs detached; first and fourth walking legs from female in Rathbun (1918b); 5 mm. indicated.

tooth somewhat obscured by ventrally bent pterygostomian lobe, sharp pointed at tip; outer lobe slightly convex. Posterior margin preceded by a tuberculate ridge.

Chelipeds in both sexes somewhat unequal, right hand approximately twice as wide as left. Walking legs short and broad; first three meral articles with a large, flat, acute distal spine, posterior distal tooth of merus sharp; carpal lobes prominent, distal one of second and third legs acute; propodus of second and third legs widening distally, dactyls wide, posterior margin sinuous.

Measurements.—Carapace: male, length, 10 mm., width, 10 mm.; female, length, 10 mm., width, 11 mm.

Habitat.—Thirty-two to 51 fathoms.

Type locality.—Off Cape Hatteras, N.C., 49 fathoms.

Known range.—Type locality; off Jacksonville, Fla.; off Yucatan, Mexico; off Cabo Frio, Rio de Janeiro, Brazil (?).

Family Grapsidae

Front quite wide; carapace usually quadrilateral, with lateral borders either straight or slightly arched, and orbits at or near anterolateral angles. Buccal cavern square; generally a gap,

often large and rhomboidal, between external maxillipeds. Male openings sternal. Palp of external maxillipeds articulating either at antero-external angle or at middle of anterior border of merus, exognath either slender or broad. Inter-antennular septum broad. Division of orbit into two fossae accented (Rathbun, 1918b).

KEY TO SUBFAMILIES, GENERA, AND SOME SPECIES IN THE CAROLINAS

- a. Antennules folding beneath front of carapace in usual way.
 - b. Third maxillipeds without a pubescent oblique ridge.
 - c. Lower border of orbit running downward toward buccal cavern (Subfamily Grapsinae).
 - d. Carapace decidedly broader than long.
 - Pachygrapsus transversus* (p. 217).
 - dd. Carapace about as long as broad; legs strongly fringed with hairs.....*Planes minutus* (p. 218).
 - cc. Lower border of orbit not running downward toward buccal cavern, but supplemented by remote suborbital crest in line with anterior border of epistome (Subfamily Varuninae)
 - Euchirograpsus americanus* (p. 220).
 - bb. Third maxillipeds with an oblique pubescent ridge crossing ischium and merus (Subfamily Sesarminae)
 - Sesarma* (p. 221).
 - aa. Antennules visible dorsally in deep clefts in front of carapace (Subfamily Plagusinae).
 - b. Carapace broader than long
 - Plagusia depressa* (p. 223).
 - bb. Carapace longer than broad
 - Percnon gibbesi* (p. 224).

Subfamily Grapsinae

Front usually strongly deflexed. Lower border of orbit running downward toward buccal cavern. Antennal flagellum very short. External maxillipeds usually separated by a wide rhomboidal gap, not traversed by an oblique hairy crest; palp articulating at or near anteroexternal angle of merus; exognath narrow and exposed throughout. Male abdomen filling all space between last pair of legs (Rathbun, 1918b).

Genus *Pachygrapsus* Randall, 1840

Rathbun, 1918b, p. 240.

Pachygrapsus transversus (Gibbes). Mottled shore crab

Figure 202.

Grapsus transversus Gibbes, 1850, p. 181.

Pachygrapsus transversus: Rathbun, 1918b, p. 244, pl. 61, figs. 2-3 (rev.).—Hay and Shore, 1918, p. 447, pl. 36, fig. 9.

Recognition characters.—Small species. Carapace rectangular, about one-fourth broader than



FIGURE 202.—*Pachygrapsus transversus* (Gibbes). Animal in dorsal view, legs of left side not shown, 5 mm. indicated.

long, depressed, polished, with fine transverse plications, except oblique ones on branchial regions. Sides slightly arched, strongly converging posteriorly, and armed with a well-marked tooth behind orbital angle. Front slightly more than half as wide as carapace, edge sinuous and granulate, upper surface with four low elevations. Orbits oblique, approximately two-fifths width of front, lower border denticulate.

Chelipeds equal, much stouter than legs, 1.6 times longer than carapace in male, finely granulate; inner edge of merus produced in a laminate, toothed expansion; meri of all legs and carpus of cheliped transversely striated; carpus with blunt internal tooth; upper surface of palm with a marginal line, oblique striae on inner and lower side, an oblique line on outer surface near lower edge; fingers narrowly gaping except for large triangular tooth near middle of immovable finger. Merus of walking legs with posterodistal angle dentate; first and fourth walking legs subequal, second and third pairs longer and subequal, last three articles bristly and thorny. Female with conspicuous feathery hairs on carpus and propodus of first walking legs.

Male abdomen with telson broadly triangular.

Measurements.—Carapace: male, length, 11 mm.; width, 14 mm.

Color.—Variable; ground color almost black, olive green, yellowish, yellowish brown or dull gray, covered by irregular mottlings of dark brown, reddish or dark olive; usually darkest an-

teriorly with transverse ridges edged with greenish gray, reddish or dark brown; chelae often plain or reddish brown, tips light; walking legs brown or blackish with gray spots (various authors).

Habitat.—This species is found among rocks, on pilings, on roots of mangroves, and on sandy shores.

Type locality.—Key West, [Fla.].

Known range.—Cape Lookout, N.C., to Montevideo, Uruguay; Bermuda. Beyond this region the species has a wide distribution in tropical and subtropical seas and has been carried to higher latitudes than it normally inhabits by transport on ships' bottoms.

Remarks.—At Bermuda, where this crab is abundant, ovigerous females have been observed from April to July (Verrill, 1908). Ovigerous females have been reported from February to August in various parts of the Caribbean area (Rathbun, 1918b, in part), and are known from North Carolina in August and September. Lebour (1944) illustrated some of the larval stages of this species from their occurrence at Bermuda.

Pearse (1932b) reported the protozoan *Epistylis*, and Verrill (1908) the isopod *Leidyia distorta* in the gill cavities of this crab.

In the past, occurrence of this crab in the Beaufort, N.C., area has been irregular and these intrusions from more southerly waters may reflect annual variations in temperature or occasional transport on vessels. As Verrill (1908) suggested, the range of this species may have been greatly extended by commerce in modern times.

Genus *Planes* Bowdich, 1825

Rathbun, 1918b, p. 253.—Chace, 1951.—Hemming, 1958b, p. 36.

Planes minutus (Linnaeus). Gulf weed crab; turtle crab; Columbus crab

Figure 203

Cancer minutus Linnaeus, 1758, p. 625.

Planes minutus: Hay and Shore, 1918, p. 448, pl. 36, fig. 6.—Chace, 1951, p. 81, figs. 1a, 2 a, d, g, j, k, l, 3 a-h (rev.).—Holthuis, 1959, p. 240.

Recognition characters.—Carapace approximately as wide as long, subquadrate in young, trapezoidal in medium sized, laterally convex in old individuals, convex dorsally, smooth, but with faint oblique lines on outer part of branchial region. Front approximately half as wide as cara-



FIGURE 203.—*Planes minutus* (Linnaeus). Male in dorsal view, approximately $\times 2$ (after Chace, 1951).

pace, decurved, usually slightly emarginate in middle, edges minutely denticulate or smooth. Eyes large; orbits large, lower margin granulate, tooth at inner angle equilateral, subacute, outer angle spiniform, behind it a small sinus.

Chelipeds large and heavy; merus and ischium with a thin serrate crest along inner margin terminating in two or three spines at distal end of merus; carpus with a strong blunt spine on inner face; hands inflated and smooth except for small sharp granules near lower margin; immovable finger bent downward, especially in males, dactyl curved, both with blunt teeth throughout length. Walking legs long, slender, and flattened; second and third legs subequal, fourth legs shortest; meri occasionally with an inconspicuous anterior subterminal tooth and a few posterior denticles; last three articles thorny and with a dense fringe of hair on anterior edge.

Abdomen of male rather broadly triangular; telson rather narrowly triangular, approximately as long as basal width.

Measurements.—Carapace: male, length, 19 mm., width, 19 mm. Length of a large series reported by Chace (1951), 3.7 to 19 mm.

Color.—Extremely variable; irregularly mottled or blotched with light greenish yellow or pale yellow on a darker olive-green ground color; or reddish-fawn color, more or less blotched with dark brown, and usually with a small white spot on each side or one large white spot on front of carapace (various authors).

Crozier (1918) observed no color change in a mahogany-colored *P. minutus* placed for a day

on a lighter background. Hitchcock (1941) found three types of chromatophores in *P. minutus*: white, black, and yellow. The most prominent chromatophore is white. Color adaptation to different backgrounds is slow and though the chromatophores are responsive to change in background, extracellular pigment in the hypodermis and exoskeleton prevents the animal from effecting an immediate change in appearance. Hitchcock concluded that the pattern of the individual crab is probably genetic. Chace (1951) remarked that in view of these findings, the apparent color of any individual can be changed only at the time of molting.

Habitat.—These crabs are more abundant on *Sargassum* in the Sargasso Sea than elsewhere, but throughout their range they depend on flotsam, or on floating or swimming organisms to which they cling (Chace, 1951).

Type locality.—On sargasso and other submarine sea plants on the north side of Jamaica (Sloane in Holthuis, 1959).

Known range.—Atlantic Ocean south of Newfoundland, west of 50° W. latitude, and exclusive of the Gulf of Mexico (Chace, 1951); Netherlands coast, North Sea (van den Oord and Holthuis, 1959).

Remarks.—The genus *Planes* has been thoroughly reviewed by Chace (1951), and the serious student should consult this paper. Chace included remarks on relative growth, stating that . . .

The carapace length-width relationship remains fairly constant with a slight tendency toward narrowing, from the smallest immature specimens examined to a carapace length of about 11 mm. At this stage the carapace seems to become somewhat narrower rather abruptly and continues to become narrower at a slightly more rapid rate than during the younger stages. A similar, but even more striking, trend is noticed in the relative shortening of the walking legs.

Chace conjectured that the specimens larger than about 11 mm. are found on flotsam and turtles rather than on sargassum, and that the shorter legs may be more adapted to this existence than to life on floating weed. It is also possible that these sizes represent different forms of *Planes* with somewhat different habits, but Chace deferred such a designation until a time when more material is available for study.

Both Hyman (1924b) and Lebour (1944) illustrated some larval stages of *Planes minutus*. In the region of the Carolinas, ovigerous females have been taken virtually throughout the year.

Subfamily Varuninae

Front moderately or little deflexed, sometimes sublaminar. Branchial region with downward sloping posterolateral portion set off from rest of region by a more or less distinctly marked line. Suborbital crest, supplementing defective lower border of orbit, rather distant from orbit and usually running in a line with anterior border of epistome. Antennal flagellum usually of good length. External maxillipeds moderately or slightly gaping, without oblique hairy crest; palp articulating with middle of anterior border or near anteroexternal angle of merus; exognath in American genera rather narrow, sometimes partly concealed. Male abdomen rarely covering all space between last pair of legs (Rathbun, 1918b).

Genus *Euchirograpsus* Milne Edwards, 1853

Rathbun, 1918b, p. 281—Hemming, 1958b, p. 31.

Euchirograpsus americanus Milne Edwards

Figure 204

Euchirograpsus americanus Milne Edwards, 1880, p. 18.—Rathbun, 1918b, p. 282, text-fig. 144, pl. 74.—Hay and Shore, 1918, p. 448, pl. 36, fig. 7.—Garth, 1946, p. 511, pl. 85, figs. 5–6.

Recognition characters.—Carapace slightly broader than long; sides nearly straight and parallel, flattened posteriorly, sloping gently down toward sides and front; surface covered with granules and short, soft hair. Front somewhat produced, lamellate, with a narrow median notch. Eyes large; orbits large, a small tooth at inner angle; upper margin oblique, sinuous; outer angle spiniform, behind it three smaller spines on lateral margin, middle spine largest; lower margin of orbit denticulate. Third article of antennae hollowed out on inner side.

Chelipeds stout, 1.5 times as long as carapace; merus with surface crossed by fine granulated lines, margins spinulose, a superior subdistal spine; carpus with inner distal margin spinulose; hand with three spinulose ridges above, a ridge near lower edge, and another less distinct through middle; fingers slender, grooved, pointed, grip-



FIGURE 204.—*Euchirograpsus americanus* Milne Edwards. Animal in dorsal view, walking legs of left side not shown, 5 mm. indicated.

ping edges with low, irregular teeth fitting together. Walking legs slender, compressed, hairy; second pair over twice length of carapace; all meri crossed by fine granulated lines and with three subdistal spines, one above, one inner, and one outer below, first merus spinulose below; dactyls armed with long spines.

Measurements.—Carapace: female, length, 14 mm.; width, 16 mm.

Color.—Yellowish gray, arranged in marblings on carapace and in alternately light and dark bands on legs, or light brown with five or six bands of red on legs (various authors). More detail given by Garth (1946).

Habitat.—Seventeen to 278 fathoms.

Type locality.—Barbados, 69 fathoms, Blake station 278.

Known range.—Off Oregon Inlet, N.C., through West Indies to Barbados, and through Caribbean Sea to Monosquillo [Morrosquillo], Colombia; Galapagos Islands.

Remarks.—This species had rarely been taken off the Carolinas until recently. Offshore collecting has shown it to be not uncommon, and a northern, as well as upper bathymetric record, was established when an ovigerous female was taken off Oregon Inlet, N.C., at 17 fathoms in February (Cerame-Vivas, Williams, and Gray, 1963). Ovigerous females are otherwise known in Florida from March to September.

Subfamily Sesarminae

Front strongly deflexed. Lower border of orbit commonly running downward toward angle of buccal cavern. Side walls of carapace finely reticulated with granules and hairs or hairs only. External maxillipeds separated by a wide rhomboidal gap, an oblique hairy crest traversing them from a point near anteroexternal angle of ischium to a point near anterointernal angle of merus; palp articulating either at summit or near anteroexternal angle of merus; exognath slender and either partly or almost entirely concealed. Male abdomen either filling or not quite filling all space between last pair of legs (Rathbun, 1918b).

Genus *Sesarma* Say, 1817

Rathbun, 1918b, p. 284.

KEY TO SPECIES IN THE CAROLINAS

- a. Lateral margin of carapace sinuous; last three articles of first three walking legs tomentose; body strongly convex above-----*reticulatum* (p. 221).
aa. Lateral margin of carapace straight; walking legs not tomentose; body nearly flat above---*cinereum* (p. 222).

Sesarma (*Sesarma*) *reticulatum* (Say)

Figure 205

Ocypode reticulatus Say, 1817, p. 73, pl. 4, fig. 6.

Sesarma reticulatum: Rathbun, 1918b, p. 290, pl. 77 (rev.).

Sesarma reticulata: Hay and Shore, 1918, p. 448, pl. 36, fig. 12 (rev.).

Recognition characters.—Carapace about four-fifths as long as broad, convex, regions distinct, surface punctate and with scattered clumps of setae above and in front; sides concave behind widest point, convergent at orbital angles. Posterolateral regions obliquely striated and setose; inferolateral and frontal regions with irregular

rows of tubercles bearing short, curved hairs. Dorsal portion of carapace overhanging sides; beneath projecting shelf a line of cilia. Lower surface of carapace covered with fine net of geniculate hairs. Front broad, slightly sinuate above basal articles of antennae. Eyestalks short and stout, set in deep oval orbits; a deep gap below outer orbital angle leading into system of grooves opening into a notch at anterolateral angle of buccal cavern. External maxillipeds separated by a wide rhomboidal gap largely filled by a hairy fringe, and obliquely traversed by a conspicuous line of hairs from point behind anteroexternal angle of ischium to anterointernal angle of merus.

Chelipeds stout, subequal in male; merus and carpus lightly rugose; merus with an obtuse subterminal tooth above, both lower margins denticulate; carpus with inner angle rounded. Palm almost smooth, in male a little higher than midlength, upper edge with a single granulate line, inner surface with a short irregular ridge of tubercles near distal end; dactyl with seven to nine depressed spinules above on basal two-thirds; fingers agape, an enlarged tooth near each end. Palm of female half again as high as midlength, fingers slightly agape. Third pair of walking legs approximately twice as long as carapace, last three articles densely tomentose.

Measurements.—Carapace: male, length, 23 mm.; width, 28 mm.

Color.—Carapace dark olive, nearly black or purple; dark plum colored or bluish-black speckles crowded on grayish background, grayish color showing little except on posterior part; upper part of chelipeds similarly colored but brighter, greater part of palm yellowish, tips of fingers white or yellowish; upper part of legs as carapace; under parts grayish (various authors).

Habitat.—Burrows in muddy salt marshes.

Type locality.—Muddy salt marshes [east coast of United States].

Known range.—Woods Hole, Mass., to Calhoun County, Tex.

Remarks.—Ovigerous females have been reported from Massachusetts in July, and in summer months farther south on the coast. Crichton (1960) found 8,000 to 10,000 eggs per egg mass.

Hyman (1924b) described the first zoeal stage and compared it with *S. cinereum*. Recently, Costlow and Bookhout (1962a) described the complete

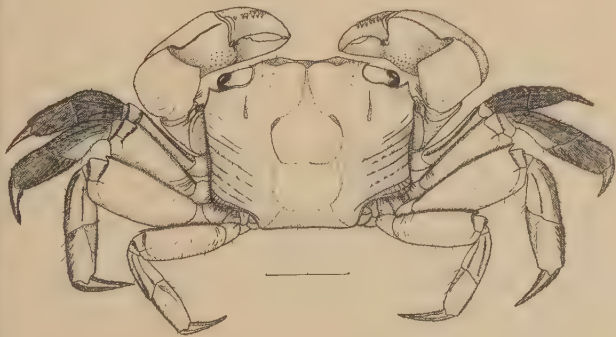


FIGURE 205.—*Sesarma* (*Sesarma*) *reticulatum* (Say).
Animal in dorsal view, 10 mm. indicated.

larval development listing three zoeal stages and one megalops stage, and compared these to similar stages they had previously described for *S. cinereum*. The authors also concluded that photoperiod has no observable effect on development.

Crichton (1960) studied a colony of *S. reticulatum* in Delaware. With the aid of rubber casts, he found that the species digs burrows which may have several openings leading at a gentle slope to a depth of 3 or 4 inches where a series of more or less level corridors curve, twist, and often interconnect. Each corridor usually leads to a vertical shaft as much as 30 inches deep and usually filled with water. Burrows are communal, containing a male or two and several females. Crichton found that this species will eat fiddler crabs (the burrows occasionally intersect) when it can capture them; however, the usual diet is *Spartina*, and swaths often are cut through this marsh grass. Burrowing action of the crab tills the land, increases erosion, and turns over the cord grass more rapidly than the annual decay cycle could do it unaided.

Teal (1959) found this species active on Georgia marshes when the tide was high or the sky cloudy. When the marsh was exposed, the crabs were found in burrows, usually near the top, in air or water. Respiration rates were higher in water than in air. Gray (1957) found the gill area of *S. reticulatum* to be relatively low as compared with other species living in a similar habitat (*Uca pugnax* and *minax*). He found *S. reticulatum* to be more robust but less active than the close relative, *S. cinereum*.

Humes (1941) described a harpacticoid copepod (*Cancerincola plumipes*) from the gill chambers of this crab.

***Sesarma (Holometopus) cinereum* (Bosc).** Wharf crab; wood crab; friendly crab; square-backed fiddler

Figure 206

Grapsus cinereus Bosc [1801 or 1802], p. 204, pl. 5, fig. 1.
Sesarma cinereum: Rathbun, 1918b, p. 300, text-fig. 149, pl. 83 (rev.).

Sesarma cinerea: Hay and Shore, 1918, p. 449, pl. 36, fig. 11.

Recognition characters.—Carapace rectangular, nearly uniform in width throughout; regions well marked; surface nearly smooth, punctate, rough with squamiform tubercles toward front; supra-frontal lobes well marked, inner pair widest. Front 4 times as wide as high, widening below,



FIGURE 206.—*Sesarma (Holometopus) cinereum* (Bosc). Animal in dorsal view, 5 mm. indicated.

somewhat four-lobed in dorsal view, lower edge sinuous. Outer orbital angle acute. Lower surface of carapace covered with fine net of geniculate hairs.

Chelipeds heavy; merus and carpus covered with short transverse lines of scabrous granules; merus with upper edge sharp, inner edge irregularly dentate with a triangular laminar expansion on distal half; carpus with inner angle rounded. Palm nearly twice as high as upper length; outer surface covered with scabrous granules arranged in parallel lines near upper margin; inner face coarsely granulate, with short prominent ridge near distal end; fingers gaping narrowly, largest tooth at middle of immovable finger. Walking legs rather narrow, meri with a superior subdistal spine; third pair of legs over twice as long as carapace.

Abdomen of male broadly triangular; telson much narrower than sixth segment.

Measurements.—Carapace: male, length, 18 mm., width, 20 mm.; female, length, 20 mm., width, 23 mm.

Color.—Brown varying toward olive.

Habitat.—Found actively crawling about on wharves and stone jetties or resting in shallow burrows above tidemark along the shores. The crabs have often been found on vessels along the coast hiding anywhere out of sight or reach and coming forth at night to feed.

Type locality.—"La Caroline."

Known range.—Magothy River, Chesapeake Bay, Md., to British Honduras; West Indies to Venezuela.

Remarks.—This species is abundant where it occurs in the Carolinas. Ovigerous females occur

from May to November in North Carolina, and have been found along the Potomac River in January (U.S. National Museum records). Hyman (1924b) briefly described the first zoeal stage. Costlow and Bookhout (1960) described 4 zoeal stages and 1 megalops stage from 1,200 zoeae reared on *Artemia* nauplii and *Arbacia* eggs under constant conditions of temperature, salinity, and light. Costlow, Bookhout, and Monroe (1960) found that optimum salinities exist for each larval stage, but that development proceeds best in the 20–26.7 ‰ range (among those tested). Temperature was found to have more effect on length of larval development than on mortality, with higher temperature speeding development. No “extra stages” were observed. The authors concluded that salinity is the chief physical factor confining *S. cinereum* to estuaries.

Pearse (1929) found that this species can survive for a considerable period of time in dilutions of sea water and also that it shows considerable resistance to desiccation. Oler (1941) maintained captive specimens from a Maryland tidal river in a house basement for about a year. The animals burrowed in mud in an aquarium where the only moisture provided was tap water. Vegetable matter was fed at irregular intervals. After several months, the larger animals ate the smaller ones, presumably at the time of ecdysis. Duncker (1934), in Germany, secured three live female *S. cinereum* which had been transported by chance in a cargo of logs from the West Indies. The animals were kept alive in a glass jar with damp peat and a container for a source of fresh water. One lived 4 years and 72 days from date of captivity. The crabs were fed shredded beef or fish and commercial fish food plus Collembola that appeared in the jar. All eating was done on land. Some regeneration of lost appendages occurred, and the longest lived specimen molted four times, molting always taking place in water. To the author's surprise, eggs were released six times, always in water, the longest lived female producing five of these batches. Larvae hatched from all but one of the egg masses, but survived only a short time. Duncker concluded that one mating was effective for 3 years or more. The incubation period was approximately 30 days. The female ate eggs that protruded over the edge of the abdomen. The number of eggs ranged from about 4,700 to 13,400

per sponge. Duncker considered that *S. cinereum* acted more like a land animal than a water-inhabiting animal, each individual having its own burrow.

Teal (1959) implied the same conclusion, for in experiments under water this species was relatively inactive, thus holding its oxygen consumption down. There was some experimental evidence for thermal acclimation of metabolism, but more evidence for acclimation by selection of microclimate. Gray (1957) also emphasized the terrestrial habits of the species, but showed that its relative gill area is nearly double that of the similar species *Ocypode quadrata*.

Subfamily Plagusiinae

Front cut into lobes or teeth by antennular clefts visible in dorsal view. Lower border of orbit curving down into line with prominent anterior border of buccal cavity. External maxillipeds neither completely closing buccal cavity nor leaving wide rhomboidal gap, not crossed by an oblique hairy crest; palp articulating near antero-external angle of merus, often no flagellum on exposed exognath. Antennal flagella short. Male abdomen filling all space between last pair of legs (Rathbun, 1918b.).

Genus *Plagusia* Latreille, 1804

Rathbun, 1918b, p. 331.—Monod, 1956, p. 455.

Plagusia depressa (Fabricius)

Figure 207

Cancer depressus Fabricius, 1775, p. 406.

Plagusia depressa: Rathbun, 1918b, p. 332, text-fig. 154, pl. 101 (rev.).—Monod, 1956, p. 455, figs. 614–617 (rev.).

Recognition characters.—Carapace subhexagonal, wider than long, depressed, covered with flattened tubercles margined with short setae. Regions distinct; front of gastric region with a series of approximately six, prominent, acute tubercles arranged in an arc. Indefinite front broad, with a deep median furrow and deep notches for antennules; a spiniform tubercle on each side between median furrow and antennular notch. Orbits deep; outer orbital angle produced into a strong, curved spine followed on anterolateral margin by three similar spines of diminishing size. Epistome prominent beyond anterior border of carapace and usually cut into five lobes.

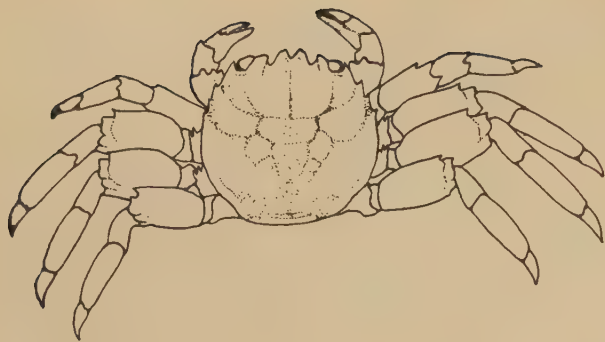


FIGURE 207.—*Plagusia depressa* (Fabricius). Animal in dorsal view (after Rathbun, 1933).

Chelipeds of adult male massive, approximately as long as carapace, in female slender, three-fourths as long as carapace; chelipeds and legs rugose dorsally; merus with three small spines above at distal end; carpus with inner angle densely dentiform; palm and dactyl with tubercles arranged in longitudinal ribs, outer surface smooth. Walking legs strong, increasing in size from first to third, fourth shorter than second; second and third legs with a dentate crest above on coxae; meri with subterminal spine on anterior border; distal three articles with a dense strip of long hair; dactyls with two rows of strong spines on concave side.

Measurements.—Carapace: large female, length, 45 mm.; width, 49 mm.

Color.—Light reddish, dotted with blood red, tubercles bordered with blackish cilia with extremity gray; blood-red spots on legs; underside of body yellowish (Latreille in Rathbun, 1918b).

Habitat.—This species is found among rocks, on jetties, in tide pools, and is thought to be transported on ships' hulls.

Type locality.—"In mari mediterraneo."

Known range.—Beaufort, N.C. through West Indies to Pernambuco, Brazil; Bermuda; Azores; Madeira; West Africa, from Senegal to Gold Coast.

Genus *Percnon* Gistel, 1848

Rathbun, 1918b, p. 337.—Hemming, 1958b, p. 35.

Percnon gibbesi (Milne Edwards). Spray crab

Acanthocarpus gibbesi Milne Edwards, 1853, pp. 146 and 180.

Percnon gibbesi: Rathbun, 1918b, p. 337.—Schmitt, 1939, p. 24.

Recognition characters.—Carapace thin, disc-like, longer than wide, covered with small short

bristles except for bare raised patches; dorsal surface with a few low tubercles. Front deeply cut by antennular furrows; portion between antennules narrow and extended in form of a rostrum, armed with two erect spines on each side distally and a row of inconspicuous spinules just within and parallel to each margin proximally. Eyes large, reniform. Inner margin of orbit bearing three spines, two distal spines prominent; middle of upper orbital border more or less serrate. Anterolateral border of carapace with four acute spines counting large spine on outer orbital angle; second spine in series with its lateral margin shorter than that of third spine.

Chelipeds varying in size with age and sex, small in females but large and unequal in adult males; merus and carpus armed with spines; palm nearly smooth, oval, and somewhat compressed, proximal upper surface with an ill-defined groove extending one-third length of upper margin, groove filled with pubescence; fingers short, blunt, with tips concave on opposed surfaces. Meral article of each walking leg with large uniform spines on anterior margin, upper surface covered with short bristles similar to carapace; posterior margin ending in a distal spine; merus of first two legs with a second row of spinules parallel with anterior border, row indistinct on third merus and absent on fourth.

Measurements.—Carapace: male, length, 30 mm., width, 28 mm.; female, length, 33 mm., width, 34 mm. (Garth, 1946).

Color.—Carapace and meral articles of walking legs brown or mottled above; usually a median longitudinal stripe of white or pale blue; legs banded with reddish, brown, and light pink distally; eyestalks and chelae orange; ventral side of body pale blue with legs pale pink (Garth, 1946; Verrill, 1908).

Habitat.—The usual habitat for this species is the underside of rocks at the low-tide level (Verrill, 1908), or in the surf at knee to hip depth, where it is extremely difficult to capture because of its propensity for rapidly keeping to the underside of turned objects (Garth, 1946).

Type locality.—Antilles.

Known range.—Fort Macon, N.C.; southern

Florida and Bahamas to Brazil; Bermuda; Azores to Cape of Good Hope; Cape San Lucas, Lower California, to Chile; Galapagos Islands.

Remarks.—Two immature females found on the Fort Macon, N.C., jetty in August 1963, by R. A. Heard, are referred to this species on the basis of characters given by Schmitt (1939) in his key to species of the genus *Percnon*. It is impossible to refer the descriptions of Rathbun (1918b) and Verrill (1908) to this species or *planissimum* with certainty, and the figures given by them also are not adequate for this purpose; but on the basis of a Bermuda specimen collected in 1962, Verrill's material was probably *P. gibbesi*.

Failure to record this species from North Carolina prior to this time is probably because there are few suitable habitats along this coast. There are few natural rocks on the North Carolina coast.

Family Ocypodidae

Palp of external maxillipeds coarse, articulating at or near anteroexternal angle of merus; exognath generally slender and often somewhat concealed. Front usually of moderate width, and often a somewhat deflexed narrow lobe. Orbits occupying entire anterior border of carapace outside front, and with their outer wall often defective. Buccal cavity usually large and somewhat narrower in front than behind, external maxillipeds often, but not always, completely closing it. Abdomen of male narrow. Male openings sternal (Rathbun, 1918b).

Genus *Ocypode* Weber, 1795

Rathbun, 1918b, p. 366 (described).—Monod, 1956, p. 390 (synonymy).

Ocypode quadrata (Fabricius). Ghost crab; sand crab

Figure 208

Cancer quadratus Fabricius, 1787, p. 315.

Ocypode albicans: Rathbun, 1918b, p. 367, pls. 127–128 (rev.).—Hay and Shore, 1918, p. 450, pl. 37, fig. 1.

Ocypode quadrata: Holthuis, 1959, p. 259.

Recognition characters.—Carapace quadrilateral, convex above from front to back, sides nearly vertical; dorsal region finely granulate on middle and posterior portions, coarsely granulate toward sides, center of carapace with a well-marked H-shaped depression. Front and side margins raised, beaded, or serrulate, lateral margin continued into

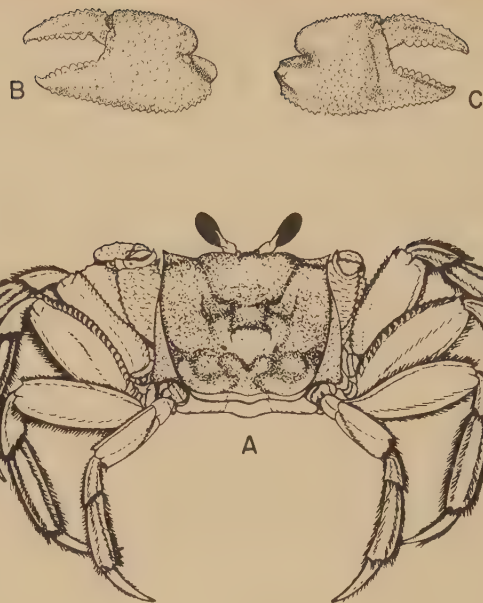


FIGURE 208.—*Ocypode quadrata* (Fabricius). A, female in dorsal view, reduced (after Gmitter and Wotton, 1953); major chela of male, B, outer view, C, inner view, reduced (after Crane, 1941).

a prominent, acute angle at outer corner of orbit; a similar but lower ridge extending upward and forward from base of third walking leg. Orbits large and open, extending all along anterior margin on either side of narrow front, both upper and lower margins crested and dentate. Eyestalks large, club-shaped, cornea covering over half of distal article. Front deflexed; antennules and antennae much reduced, flagellum of antennules hidden beneath front.

Chelipeds in both sexes, and in young, unequal, well developed, rough; merus serrulate above, toothed on lower margins; carpus with sharp spines at inner angle; hands coarsely scabrotuberculate, margins of palm and fingers dentate, fingers pointed. Large hand with a vertical stridulating ridge of tubercles on inner surface near base of movable finger that plays against smooth, distal, anteroventral ridge of ischium. Walking legs almost smooth, fringed with long, stiff, yellow hair, third pair longest, fourth shortest; meri of first three pairs broadened; propodi of these legs with longitudinal brushes of hair on anterior surface; dactyls of all legs fluted, depressions hairy.

A hair-fringed breathing slit on ventral surface between basal articles of third and fourth walking legs.

Measurements.—Carapace: male, length, 44 mm.; width, 50 mm.

Color.—Gray, pepper-and-salt, grayish white, pale yellow, straw color, or yellowish white imitating color of beaches; sometimes light amber and often iridescent; yellow markings below and on legs; young mottled gray and brown (various authors).

Habitat.—This species, the most terrestrial of the decapod crustaceans in the Carolinas, lives in abundance along the ocean beaches and sometimes on harbor beaches. The crabs construct burrows 2 to 4 feet in depth from near the high-tide line to distances up to a quarter of a mile from the ocean.

Type locality.—Jamaica.

Known range.—Block Island, R.I., to State of Santa Catarina, Brazil (megalops have been taken at Woods Hole).

Remarks.—The ghost crabs are so large, accessible, and widely distributed that they have been extensively investigated in various parts of their range.

Perhaps because of its mode of life, this animal has left a fragmentary fossil record. Rathbun (1935) recorded *O. quadrata* questionably from the Pleistocene of Florida. Hayasaka (1935) compared the "sandstone pipes" commonly found in certain Tertiary sandstones of Formosa to plaster casts of burrows made by the Formosan crab, *O. ceratophthalma*, and found them to be much alike. Burrows of the modern Formosan and eastern North American species are similar.

The egg-laying season in the Carolinas appears to extend from April (Coues, 1871) to July. Apparently the egg-bearing period is approximately the same farther south at Tortugas, Fla. (Cowles, 1908), and farther north in New Jersey (Milne and Milne, 1946). The latter authors pointed out that ovigerous females differ in behavior from other individuals in that they wade in water more freely, run along on the bottom, and at intervals when the water is quiet open the abdomen out, flip upside down, extend the mouthparts, rotate the legs, and, thus, force water through the egg mass. Such females will run quickly to water when disturbed. The free-swimming zoea of this

species has not been described, but the megalops was first described by Say (1817) as *Monolepis inermis*. Smith (1873a, 1873b, 1880b) recognized the true status of the form, and pointed out that though this megalops is carried as far north as Vineyard Sound by the Gulf Stream, that area is apparently too cold to support an adult population.

Habits of *O. quadrata* have been treated in a number of scholarly and popular works, but the serious student is referred especially to Cowles (1908) and Milne and Milne (1946). A popular account of some value, except for the concluding conjectures, was given by Phillips (1940). Only a brief summary from these authors can be given here.

The young crabs are found close to shore. Burrows of the young are near the water and extend to water level or are covered by high tides for a time, whereas older crabs burrow farther from water; such burrows seldom are deep enough to reach water level. Burrows are of three general types: (1) a short vertical burrow made by young crabs, (2) a burrow sloped downward at about 45 degrees away from the shoreline, often with a vertical branch extending upward almost to the surface, and (3) burrows higher on the beach, much like the second type but without the vertical side branch. In fall in New Jersey, the burrows were found to be farther from water and far deeper than any studied earlier in the year, and it is presumed that a variety of sizes of crabs hibernate in these deep burrows.

Burrow making is primarily an occupation of daylight hours. The crabs cease feeding on the wet beach toward dawn. Those feeding on a fish carcass often burrow within an inch or two of the carcass. Young crabs near water make new burrows, older ones range inland and build burrows or occupy old holes. Sand is brought to the mouth of the burrow and dropped or spread near the opening in a fan-shaped area. Toward noon, openings to burrows are plugged with damp sand, thus concealing the burrow. Toward evening the crabs begin to emerge again, and by 10 p.m. the whole population is usually on the beach.

These crabs are scavengers (and cannibals) and tend to feed most actively along the drift line, looking for beached fish or refuse and small bits of food buried in the top layer of sand. The crabs

do not enter the water to search for or capture food.

The crabs have to go into the water at intervals to moisten the gills, and the young do this more frequently than adults. When undisturbed, the individuals do not actually enter water but will stop a few inches from the waterline with one side presented to the water, the legs of the other side anchored in sand, and wait for a wave to wash over them after which they return to the higher parts of the beach. If disturbed, the crabs will run into the water, then leave it as soon as possible. These crabs do not swim but walk on the bottom or are rolled about by waves. The crabs can survive for a limited time if forced to remain submerged.

Locomotion is accomplished by all eight walking legs. Usually the crabs walk sideways or obliquely. If hotly pursued, the crabs will run in another manner, holding the last pair of legs clear of the ground. Usually the crabs walk or run toward the side with the small chela. This crab can also walk forward, or sometimes approach food by walking slowly backward.

The eyes of *O. quadrata* are so large and prominent that it seems as if the crab can see exceptionally well. Experiment has shown that the eyes are primarily sensitive to large changes in intensity of light. The crabs do not tend to avoid strong light, but try to hide if lights are suddenly shut off or if an object on the beach is suddenly moved. The eyes apparently aid in the search for food, but actual detection of food is by taste or smell.

There is no evidence that *O. quadrata* can hear, though a well-developed stridulating ridge is borne on the large chela. No one has reported observing this crab in the act of stridulating.

Cowles (1908) noticed that the ghost crab exhibits color changes. The crabs are generally dark in subdued light and in direct sunlight if temperature is not above 35° C. Above 35° C., the crabs are light colored regardless of light intensity. In absence of light, the crabs are light colored regardless of temperature.

The general relationship of habitat to oxygen consumption and general activity among certain Decapods has been a subject of study by Ayers (1938), Pearse (1929), Vernberg (1956), and Gray (1957) in the Beaufort, N.C., area. In all these studies, *O. quadrata* was of prime interest

because of its terrestrial adaptation combined with great activity. Of all the crabs studied in this geographic area, the ghost crab possesses the highest rate of oxygen consumption both for the whole animal and for gill tissue alone. This is more striking when it is emphasized that *O. quadrata* has a reduced number of gills (though it does have accessory respiratory tissues in the gill cavity) and the gill area per gram of weight in this species is by far the lowest among 16 species studied in near-shore, intertidal, and above-tide zones.

Flemister and Flemister (1951) and Flemister (1958) have shown that when *O. quadrata* is confined in water, oxygen consumption is elevated, but elevated least when chloride ion concentration of the water equals that of the blood. Lower or higher ion concentration of the water raises the respiration rate. They demonstrated that the animals normally have blood hypotonic to sea water. In sea water containing less than 120 or more than 160 millimoles of chloride per liter, the internal concentration is not maintained but tends to rise or fall depending on which end of this range the animal experiences. The antennal gland, aided by the gill membranes, functions in regulation of internal chloride ion concentration.

Genus *Uca* Leach, 1814

Rathbun, 1918b, p. 374.—Monod, 1956, p. 399.

KEY TO SPECIES IN THE CAROLINAS

- a. Large cheliped of male with oblique tuberculate ridge on inner surface of palm extending upward from lower margin.
 - b. A prominent transverse depression behind orbit; leg joints red on large cheliped; color dark, usually grayish toward front margin.....*minax* (p. 227).
 - bb. Without prominent transverse depression behind orbit; leg joints not red; color dark, often with blue on front.....*pugnax* (p. 229).
- aa. Large cheliped of male without oblique tuberculate ridge on inner surface of palm extending upward from lower margin.....*pugilator* (p. 232).

Uca minax (Le Conte). Red-jointed fiddler; brackish water fiddler

Figures 209A, 210B

Gelasimus minax Le Conte, 1855, p. 403.

Uca minax: Rathbun, 1918b, p. 389, pl. 137 (rev.).—Hay and Shore, 1918, p. 451, pl. 37, fig. 3.

Recognition characters.—Carapace subquadri-lateral, approximately 1.3 times as wide as long, widest behind outer orbital angles, convex in both

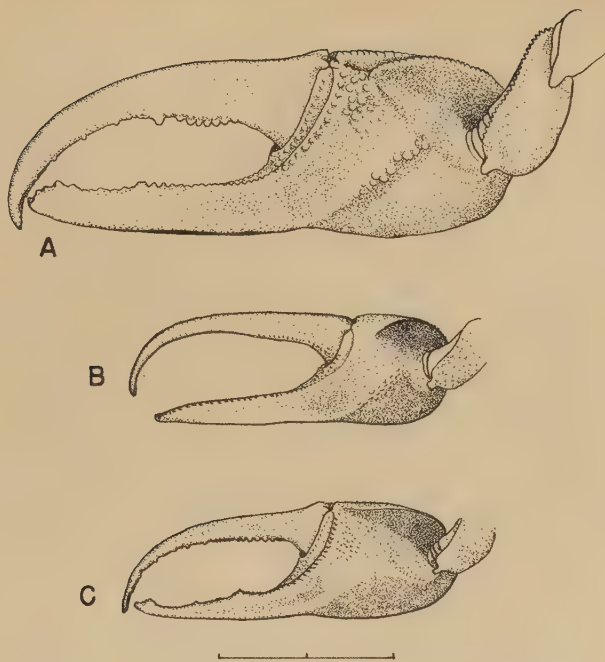


FIGURE 209.—Large chela of male, view of inner side; A, *Uca minax* (Le Conte); B, *Uca pugnax* (Smith); C, *Uca pugilator* (Bosc); 20 mm. indicated.

directions, finely granulate, except somewhat coarsely so near anterolateral angles; a shallow H-shaped depression near center of carapace, and a horizontal depression behind orbit. Lateral margins nearly vertical; anterolateral angles slightly produced, continued backward and inward as a low, well-defined ridge, and above orbits as a low revolute ridge. Front greater than one-third frontoorbital width, broadly convex. Orbits large, open, eyebrow 5 times as wide as deep, lower margin dentate; eyestalks long, slender. Antennules and antennae small, flagellum of antennules hardly visible. Merus of second maxilliped with never more than 10 exceedingly slender spoon-shaped hairs.

Chelipeds in male very unequal, in female equal and of small size. Large chela with upper surface of merus sparingly granulate, inner edge denticulate, outer edge granulate; carpus tuberculate. Upper and outer face of large hand in male with tubercles diminishing to granules on lower face, ridged above; inner surface with an oblique row of granules from lower margin to carpal cavity, a short curved row leading down from ridge on upper margin, area between ridges tuberculate

and with a tuberculate ridge running along immovable finger from tip to internal distal border of palm. Fingers strong, with wide gape, cutting edges tuberculate; immovable finger with a few larger teeth at irregular intervals, truncate at tip; dactyl longer and curving downward past tip of opposed finger. Walking legs strong, sparsely hairy, meri slightly wrinkled.

Measurements.—Carapace: male, length, 25 mm.; width, 38 mm.

Color.—Chestnut brown, becoming gray in front; chelipeds with red spots at articulations; hands ivory white; legs olive or grayish brown.

Habitat.—This species occurs in marshes at some distance from water of high salinity. It is usually found on muddy substrates where flooding with fresh water occurs (Teal, 1958), or on a mud and sand substrate (Gray, 1942). In North Carolina, the species is found in *Spartina* marsh, often far from banks of ditches, and in the area immediately preceding the *Salicornia-Distichlis* zone (Vernberg, 1959). It has also been observed at the edge of low woodlands (Teal, 1959). The crabs live in burrows which they dig to various depths, but the maximum is about 2 feet. The openings are often considerably above high-tide level, and the bottoms reach to ground-water level. The burrows are only wide enough to accommodate the occupant. Usually only one crab lives in a burrow, though at times two females may occupy a single burrow, and burrows of females sometimes communicate with burrows of males, the connection being made by the female (Gray, 1942). Young crabs are sometimes found in the burrows of females, never in those of males.

Type locality.—Beesleys Point, N.J.

Known range.—Buzzards Bay (Wareham), Mass., to Matagorda Bay, Tex.; Colombia; Dominican Republic.

Remarks.—This species has been the subject of a number of ecological and physiological studies, undoubtedly because of its wide distribution and accessibility. It is the largest of the three species of fiddler crabs occurring on the east coast of the United States, though it is not so abundant as the other two species and its habitat is somewhat more restricted.

Spawning occurs in the Carolinas and as far north as mid-Chesapeake Bay in summer. In Chesapeake Bay, ovigerous females are most

abundant in July; none are known to occur before July or after the first week in September, and about the same length of breeding season is found in the Beaufort, N.C., area. Gray (1942) presented evidence for two spawnings per season. The act of egg laying has not been studied in minute detail, but Gray (1942) observed egg deposition among captive females held in aquaria. Completion of spawning was usually accomplished in a day but sometimes took as long as 3 days, depending on temperature. (Hyman (1920) and others have dug ovigerous females from burrows.) Freshly laid eggs were yellow or pale orange in color, but the color changed with development through a purplish-black to an ashy gray color, at which stage the larvae emerged (see also Hyman, 1920). Estimated egg counts on a number of ovigerous females ranged from 10,000 to 300,000, depending on size of the individual. Newly laid eggs measured about 0.09 mm. in diameter but increased to about 0.27 mm. at the time of hatching. Both Hyman (1920) and Gray (1942) observed that the females entered water in order to let the eggs hatch. Time of hatching extended from about 7:00 to 10:00 p.m., and the hatching of an egg mass required slightly less than an hour.

The first zoeal stage of *U. minax* is the smallest among our three species of *Uca*. The larval stages are discussed in the remarks on *U. pugnax*.

Uca minax is an omnivorous feeder but avoids highly putrified debris (Gray, 1942). Teal (1958) showed that fiddler crabs can subsist on a mixture of sand, clay, bacteria, and fermented marsh grass (natural staples in their diet), and he observed *U. minax* kill and eat *U. pugnax* and *U. pugilator* on several occasions. Contrary to the findings of others, he observed (1959) that *U. minax* can and does feed underwater. Miller (1961) compared the mouthparts of *U. minax* to those of the more specialized Carolinian *Ucas*. He found that it prefers to feed in low areas of the *Spartina* marshes well up in estuaries where mud is fluid.

In a search for factors that might limit *U. minax* to its particular habitat, Teal (1958) found that the temperatures experienced in nature had no effect on survival but that the species could live in fresh water for more than 3 weeks and, when offered fresh and salt water, *U. minax* chose

to live in fresh water. When offered a choice of mud or sand substrates, this species chose mud either above or under water, but when competitive species of *Uca* were present fewer burrows were dug. Teal (1959) found that *U. minax* had the lowest rate of oxygen consumption among a number of marsh crabs investigated (*U. pugnax* and *pugilator*, *Sesarma cinereum* and *reticulatum*, *Eurytium limosum*, and *Panopeus herbstii*) which is contrary to the argument of Ayers (1938) that the more terrestrial species have relatively higher rates of metabolism than do aquatic forms. Teal (1959) and Vernberg (1959) further observed that *U. minax* in all probability does not acclimate respiratory rate to changes in temperature. Gray (1957) found gill area per gram of body weight in *U. minax* lowest among East Coast *Ucas*, Below 20° C., this species is inactive (Gray, 1942; Teal, 1959). Gray found that *U. minax* overwinters in burrows just below the frost line.

Sexual display of the males among fiddler crabs has been a subject of much study and is too complex for complete review here. Crane (1943, 1944) dealt with this subject briefly for *U. minax*. In display, the males rear back on the last two or three walking legs so that the carapace is vertical. The major cheliped is extended diagonally up to about half of maximum extension. This position may be held for minutes, then the cheliped may be fully extended swiftly and smoothly, and finally brought back to the half-extended position in a series of jerks. This movement may be repeated about four times rather slowly. The small cheliped is moved asynchronously in similar motions.

Uca pugnax (Smith). Mud fiddler

Figures 209B, 210A

Gelasimus pugnax Smith, 1870, p. 131, pl. 2, fig. 1, pl. 4, figs. 2-2d.

Uca pugnax: Rathbun, 1918b, p. 395, pl. 139.—Hay and Shore, 1918, p. 451, pl. 37, fig. 4.—Tashian and Vernberg, 1958, p. 89 (rev.).

Recognition characters.—Carapace subquadri-lateral, approximately 1.5 to 1.75 times as wide as long, widest behind outer orbital angles, very convex anteroposteriorly, lower edge of front and upper margin of orbit invisible in dorsal view, smooth. A shallow H-shaped depression near center of carapace, a pit on branchial region in line with gastro-cardiac sulcus, and a pit behind mid-

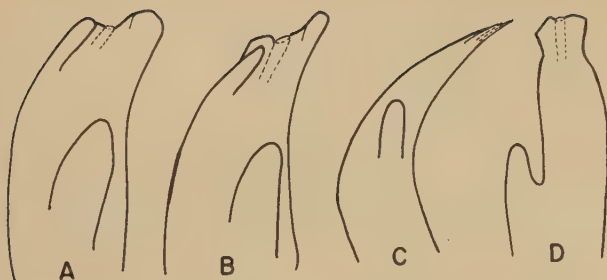


FIGURE 210.—Tips of right abdominal appendages of adult males, hairs omitted; A, *Uca pugnax*, anterior view; B, *Uca minax*, anterior view; C, *Uca pugilator*, anterior view; D, same, lateral view (after Crane, 1943).

dle of orbit. Anterolateral angles slightly produced, continued backward and inward as a low, well-defined ridge, and across entire frontoorbital width. Front about two-sevenths of frontoorbital width, margin regularly arched. Orbits large, open, upper margin sinuous and oblique, lower margin dentate. Eyestalks long, slender. Antennule and antenna small. Merus of second maxilliped with between 10 and 20, rarely 25, spoon-tipped hairs.

Chelipeds in male very unequal, in female equal and of small size. Large cheliped of male rough; merus with granulated rugose lines outside, lower margins granulate. Carpus and palm tuberculate outside; inner surface of palm with oblique row of granules leading from lower margin to carpal cavity; a short row leading down from ridge of proximal half of upper margin; area between crests coarsely granulate or tuberculate and with tuberculate ridge running along finger from tip to internal distal border of palm. Fingers long, slender, widely gaping; immovable finger usually with one large tooth near middle, inferior border nearly straight, tip sometimes depressed, truncate; dactyl evenly denticulate and with irregularly placed large tubercles, strongly curving downward past tip of opposed finger. Walking legs with carpal and propodal articles hairy.

Measurements.—Carapace: male, length, 15 mm.; width, 23 mm.

Variations.—There is a tendency toward decrease in size in the southern extremity of the range (Tashian and Vernberg, 1958).

Color.—Carapace of male dark greenish olive, middle and anterior portion mottled with grayish white; front variably light blue between and

above bases of ocular peduncles, margin tinged with brown; large cheliped lighter than carapace, pale brownish yellow at articulations and along upper edge of dactyl, fingers nearly white along opposed edges; ocular peduncles and eyes much like dorsal surface of carapace; smaller cheliped and legs somewhat translucent and thickly mottled with dark grayish olive; sternum and abdomen mottled ashy gray. Females less mottled with white dorsally, and without blue on front (various authors).

Habitat.—Pearse (1914) recorded this species as living primarily on intertidal flats of mud or clay among the roots of *Spartina*, but overlapping to some extent the sandier habitat frequented by *U. pugilator*. He found the maximum number of burrows about 2 feet below high-tide mark, and often the burrows had mud towers at the mouths when the beach was littered with debris. Crane (1943) observed "shelter building" in this species to be in its most rudimentary form among the *Ucas*. She found that in a mixed population of *U. pugnax* and *U. pugilator*, *U. pugnax* always chose the side of any surface irregularity for a hole entrance in preference to flat ground. Pearse (1914) found burrows extending to 2 feet in depth and terminating at the water level. Teal (1958) reported burrows on Georgia Sea Islands to be in situations similar to those observed by Pearse, on low levees bordering tidal creeks or farther from creeks in firm, marshy ground sometimes covered only at spring tides. Schwartz and Safir (1915) found *U. pugnax* burrows on a muddy substrate well shaded by marsh vegetation; hence, continually moist. *U. pugnax* digs most actively when the tide is falling, and often hastens to plug burrows when the tide is rising to cover the burrow mouths (Pearse, 1914).

Type locality.—New Haven, [Conn.].

Known range.—Cape Cod, Mass., to near St. Augustine, Fla. (Tashian and Vernberg, 1958); northwest Florida to Texas (Hedgpeth, 1950).

Remarks.—Like the preceding species, *U. pugnax* is an abundant and easily accessible, relatively large decapod which has received the attention of numerous students. Only information of greatest general interest can be mentioned here.

The fossil record for this species extends only into the Pleistocene of New Jersey and Delaware (Rathbun, 1935).

Ovigerous females have been observed near Woods Hole, Mass., from July 4 to July 15 (Pearse, 1914), wandering about over the ground. Farther south the spawning season is more extended, from early July to mid-August in New Jersey (Crane, 1943), and as early as May 21 at Long Lake, Tex. (Hedgpeth, 1950), and in April in northeastern Florida (U.S. National Museum records). On Long Island, N.Y., the peak of spawning occurs in August (Schwartz and Safir, 1915). Crane (1943) thought it likely that in the region near New York two breeding times occur, one in July and the other in August.

The larval and postlarval stages are discussed in the remarks on *U. pugilator*. Hyman (1920) secured ovigerous females for hatching of eggs by digging them from burrows. He found the first zoea of *U. pugnax* to resemble closely that of *U. pugilator* except for smaller size of the former.

Schwartz and Safir (1915) found the food of *Ucas* to consist largely of minute algae left on sand by the outgoing tide. Such algae were picked up by means of the small cheliped in males; females, using both small chelae, secured more food in a given time than males. The small chelipeds seemed sensitive to such food, for they were dragged along on the sand while the animals searched for food. Much sand was taken up with the food. Rapidity of movement of the small chelipeds to the mouth was timed and found to be from 24 to 26 times a minute in males, and from 74 to 92 times per minute in females. Teal (1958) found that *U. pugnax* frequently feeds underwater, and that it often remains outside burrows and feeds as the tide rises. This species can subsist on bacteria and organic debris. Miller (1961) in his well-illustrated study considered *U. pugnax* to be intermediate in development of spoon-shaped hairs on the mouth parts and, therefore, more ubiquitous in choice of feeding substrates than its congeners in the Carolinas. Great detail is given in this study.

In experiments on salinity tolerance, Teal (1958) found that 50 percent of *U. pugnax* placed in fresh water died within 1.5 days. In water of 7 ‰, 50 percent mortality occurred after 3 days. Given a choice of fresh or 30 ‰, *U. pugnax* chose salt water. Teal concluded that these data are

consistent with the general distribution of the species, which is restricted to tidal marsh.

Given a choice of sand or mud substrate above or under water, *U. pugnax* burrowed only in mud without any reference to water level, and competitive species of *Uca* had no significant effect on numbers of burrows dug. When restricted to the relatively high *Salicornia-Distichlis* marsh, *U. pugnax* survived less well than *U. pugilator*.

Respiration rates for *U. pugnax* are higher underwater than in air (Teal, 1959), probably because of increased activity necessary to ventilate the gills.

At normal habitat temperatures, *U. pugnax* (= *rapax*) from Trinidad showed a higher metabolic rate than from localities in the United States (Tashian, 1956). Tashian found that there is a decrease in sensitivity to temperature change from southern to northern populations, along with an increase in tolerance to low temperature. Teal (1958) found that temperatures experienced in nature are not limiting factors in distribution of *U. pugnax* in Georgia, though high temperatures near a lethal level occur at times in summer. He (1959) concluded that among marsh crabs studied (see "remarks *U. minax*"), *U. pugnax* exhibits the most highly developed thermal acclimation, and its abundance on the marshes may be explained in part by its ability to regulate its metabolism over a wide range of temperature. Vernberg (1959) and Vernberg and Tashian (1959) reinforced this conclusion, showing that *U. pugnax* exhibits a marked tendency to demonstrate seasonal thermal acclimation. Brett (1960) showed that the daily oxygen-consumption cycle is considerably modified by locomotion of the crabs. Gray (1957) found gill area per gram of weight in *U. pugnax* to be lowest among the East Coast *Ucas*.

Crane (1943) observed hibernating *U. pugnax* in New Jersey, where the burrows were weathered open along the muddy banks of small creeks and could only have been submerged at spring tides. In March at air temperatures of 1.7° to 5.5° C., the immobile crabs were found from the burrow mouths to about 4 inches below the surface. Slight warming in the hand or in the sun elicited fairly rapid movement.

In another vein, Passano (1960) found an inverse correlation between temperature and pro-

ecdysis duration in *U. pugnax*. Surprisingly, at some temperature between 15° and 22° C. proecdysis fails to proceed normally, though these animals experience much lower temperatures throughout their range. It was suggested that the northern limits of the species are influenced by the inability of larvae to molt in cold water; hence, adults cannot appear there.

Crane (1943) gave a detailed description of the display and breeding relationships for this species. Display of males starts with the body elevated moderately high and both chelae held well off the ground and flexed in front of the mouth. Both chelipeds are extended obliquely upward, then the major claw is returned downward in a jerk or a series of jerks with no pause between extension and flexion. The fingers usually remain nearly closed, and a complete cycle of movement usually requires about 2 seconds. (Movement of the small chela is not described.) At times males will exhibit a series of bobbings or "curtseys," especially when displaying to females. Pearse (1914) and others considered these activities to be courtship display.

Other activities which have received much attention in experiments are rhythmic cycles. Brown and his coworkers (Brown and Sandeen, 1948; Brown and Webb, 1948, 1949; Brown, Webb, Bennett, and Sandeen, 1954) showed that fiddler crabs (among them *U. pugnax*) exhibit temperature-independent, diurnal, rhythmical color changes. These rhythms may be altered, or delayed, by lowering temperature for a time, or by altering the period or time of illumination. They further demonstrated that possibly two centers of rhythmicity exist in these crabs, each capable of having its rhythm altered independently of the other, and with one center influencing the other. Brown, Fingerman, Sandeen, and Webb (1953) demonstrated that amplitude of diurnal cycles under constant conditions increased to a maximum in 2 weeks. Superimposed on diurnal cycles are tidal rhythms which persist in phase with native local conditions under constant laboratory conditions. Oxygen consumption reflects these cycles as well as a lunar cycle (Brown, Bennett, and Webb, 1954; Brown, Fingerman, and Hines, 1954; Brown, Webb, Bennett, and Sandeen, 1955). Bennett, Shriner, and Brown (1957) found that degree of spontaneous locomotor ac-

tivity is also related to tidal cycles although the rhythm persists only about a week under constant conditions.

Primarily because of the tremendous asymmetry in chelipeds of male fiddler crabs, *Uca* became an object of studies on relative growth. (In some of these papers no clear species designation was made.) In fiddler crabs [*Uca pugnax*] the percentage weight of the chela alters throughout life from 2 percent (the value retained by the female) to 65 percent (Huxley, 1927). In the related larger species, *U. minax*, since allometric growth continues longer, the chela may weigh over three-fourths of the remainder of the body (77 percent). Increasing relative size of the chela is associated with an increasing asymmetry of the central nervous system. Thus, such animals have no fixed form, for the proportions of parts are changing throughout postlarval life. On this basis, Huxley challenged Morgan's (1923) statement that females with intermediate width abdomens (subject also to allometric growth, Huxley, 1924) were actually intersexual female types. Tazelaar (1933) explored the subtleties of relative growth in *U. pugnax* in detail, finding that walking legs near the great chela and near the wide abdomen of females also reflect relative growth influences.

Uca pugilator (Bosc, [1801 or 1802]). Sand fiddler

Figures 209C; 210 C, D; 211

Ocypoda pugilator Bosc, [1801 or 1802], p. 197.

Uca pugilator: Rathbun, 1918b, p. 400, pl. 141; pl. 160, fig. 2 (rev.).—Hay and Shore, 1918, p. 452, pl. 37, fig. 2.

Recognition characters.—Carapace subquadri-lateral, up to 1.5 times as wide as long, widest behind outer orbital angles, very convex, smooth; a shallow H-shaped depression near center of carapace and a narrow, flattened shelf behind orbit. Lateral margin strongly curved outward behind orbit, continued backward and inward as a low, well-defined ridge across entire frontoorbital width. Front more than one-third of frontoorbital width, broadly rounded below. Orbits large, open, upper margin slightly sinuous, lower margin dentate. Eyestalks long, slender. Antennule and antenna small. Merus of second maxilliped with 150 to 200 spoon-tipped hairs arranged in about 10 rows on inner side.

Chelipeds in male very unequal, in females equal and small. Merus of large chela with short,



FIGURE 211.—*Uca pugilator* (Bosc). Male in dorsal view, about natural size (after Rathbun, 1884).

granulated, rugose lines above and with isolated dark hairs proximally, nearly smooth outside, lower margins granulate; merus of small chelipeds with scattered hairs. Carpus and outer surface of large hand with tubercles diminishing to granules on lower face of hand. Inner surface of palm without oblique tuberculate ridge as in *U. minax* and *U. pugnax*, but with a tuberculate ridge running along immovable finger from tip backward on internal distal border; surface granulate, granules coarser on thickest part of palm. Fingers strong, gaping; immovable finger with largest tubercles just behind middle and near truncate tip, inferior surface convex; dactyl evenly denticulate and with irregularly placed large tubercles, strongly curving downward past tip of opposed finger. Walking legs narrow.

Measurements.—Carapace: male, length, 17 mm.; width, 26 mm.

Color.—Carapace of male a dull light purplish or grayish blue of varying shades, or with irregular markings of brown or dark gray, a large patch of deep purplish blue on anterior half; large cheliped dull light blue at base with white tubercles, articulations yellowish; fingers mostly white; small chelipeds and legs buff with blue or brown speckles (various authors). Specimens from Massachusetts, bluish gray; those from Florida, reddish yellow (Démeusy, 1957).

Habitat.—This species occurs in countless numbers on sandy and muddy beaches bordering marshes, and along banks of tidal creeks. The crabs also occur farther from water in sandy situations of the *Salicornia-Distichlis* marsh and at times in *Juncus* marsh where the soil is sandy (Teal, 1958). The species burrows much as does *U. pugnax*, and populations of the two species are

often intermingled (Pearse, 1914), though *U. pugilator* prefers sandier situations (Hyman, 1922). Dembowski (1926) found that choice of a place to burrow depends upon many factors, among them phototaxis and thigmotaxis. Burrows may have any shape but are unbranched and usually dug at an angle to the surface of the ground, the length of the burrow depending in part on the amount of moisture in the ground. Digging by males is done with legs on the side opposite the large claw. The crabs plug the opening as soon as they feel the water level rising in the burrow with the tide, and do this by pulling in the edges of the burrow and by ramming sand up from below. The end chamber, thus, functions as an air chamber during high tide.

Type locality.—"Caroline."

Known range.—Boston Harbor, Mass., to Texas; Old Providence Island (Coventry, 1944); Haiti.

Remarks.—*Uca pugilator*, like its east American congeners, has been the subject of much study, and one of the most readable accounts of its natural history is that of Hyman (1922).

In the vicinity of Beaufort, N.C., ovigerous females are found in spring and early summer. In Virginia, they are known from March to July (U.S. National Museum records). Schwartz and Safir (1915) found ovigerous females at Long Island, New York, from the first week in July until mid-August; in Massachusetts, Pearse (1914) found no ovigerous specimens until the first part of August. In Texas, Hedgpeth (1950) reported zoeae taken in a plankton net on May 20 at Long Lake. The breeding season, thus, is similar to those of the species discussed above in being seasonally related to latitude. Schwartz and Safir (1915) and Hyman (1920, 1922) stated that ovigerous females were rarely seen at the surface, but Hyman found that they left their burrows to aerate the eggs in water for a time at dusk. When the eggs were ready to hatch, the zoeae were released at such time in the water.

The larval and postlarval stages of the East Coast species of *Uca* were described and illustrated by Hyman (1920) based largely on study of *U. pugilator*. Hyman could find no consistent morphological differences among each stage of the three species. Five zoeal stages and a megalops stage were described. Gray (1942) described a

transitory prezoal stage. Hyman found the first two zoeal stages most abundant at the surface, the third probably at intermediate depths, and the fourth and fifth zoeae usually on the bottom. He found the zoeal stages to last collectively about a month.

The megalops, a single stage lasting nearly a month, is a powerful swimmer. At the end of this stage the animal retires to cover of some sort, molts through two relatively weak crab stages and at last emerges as an active small crab measuring about 2 mm. across the carapace.

Feeding movements in *U. pugilator* are essentially the same as in the other two species of *Uca* and are discussed in the account for *U. pugnax*. Schwartz and Safir (1915) found the males moved the small cheliped to the mouth 28 to 46 times per minute, and females 61 to 92 times, when actively feeding on small particles in sand. Teal (1958) found that this species may wander into tide pools and shallow creeks to feed underwater at low tide. Miller (1961) considered *U. pugilator* to be the most specialized in mouth parts among Carolinian *Ucas* and well adapted to feeding on coarse substrate such as protected sandy beaches.

In experiments on salinity tolerance, Teal (1958) found that in fresh water 50 percent of *U. pugilator* died after 3.5 days. In water of 7 ‰ more than 50 percent of the animals survived a 10-day test. Given a choice of fresh or 30 ‰ sea water, *U. pugilator* chose salt water, but preferences shown by females were less strong than those shown by males, as was true also of *U. pugnax*. Teal concluded that this species lies between *U. minax* and *U. pugnax* in its tolerance of fresh water and can survive soakings of the *Salicornia* marsh with rain between spring tides.

Given a choice of sand or mud substrate above or underwater, *U. pugilator* burrowed almost exclusively in sand above water level. When either of the other species of *Uca* was present as a competitor for space, there was a reduction of 50 percent in the number of burrows that *U. pugilator* dug in sand above water. In tanks where there was no favorable substratum of sand above water, its behavior was not changed by presence of another species. When restricted to an unfavorable, low, muddy marsh, *U. pugilator* did not survive. Teal conjectured that this species cannot feed properly where sand is absent.

Respiration rates for this species are higher underwater than in air (Teal, 1959), probably due to increased activity necessary to ventilate the gills.

Teal (1958) found that temperatures of 45° C. on open sand flats of the *Salicornia-Distichlis* marsh in Georgia prevent *U. pugilator* from permanently occupying these areas, though they do feed there in cooler parts of the year. In general, temperatures experienced in nature were not considered a limiting factor. Orr (1955) found that *U. pugilator* died in 81 minutes at 40° C., in 18 minutes at 41° C., in 9 minutes at 43° C., and in a little less than 9 minutes at 46° C. Dèmeusy (1957), investigating respiratory rates in populations of this species from Florida and Massachusetts, found that the northern population had a higher rate of metabolism at low temperatures (1.4° C.) than the Florida population, but that at 15° C. the difference was not significant. Dèmeusy found the northern population less sensitive to temperature change and more resistant to low temperature than the Florida population. On the other hand, Edwards (1950) found metabolic differences in these populations at 20° C. Teal (1959) found that above 25° C. specimens from Georgia showed no adjustment of respiration for temperature acclimation, but that below 20° C. there was some evidence of acclimation though not so well developed as in *U. pugnax*. Vernberg (1959) pointed out that metabolic activity in *Uca* of the temperate zone exhibits a seasonal cycle and that this cyclic change must be taken into account in comparing physiologic activity of relatives at different latitudes. Moreover, he stated that metabolic response of fiddler crabs has real significance in their distribution.

Crane (1943) gave a detailed description of the display and breeding relationships for this species. Display of males starts with the body elevated, cheliped tips lowered, and the meral-carpal joint of the major cheliped elevated. The cheliped is then extended up and out, the crab at the same time raising to tiptoe. The cheliped is held out for an instant, then smoothly returned to the original position. The minor chela makes weak corresponding gestures and fingers of both chelae are nearly closed throughout. Waves are made at a rate of about one per second. At moments of

extreme excitement, the major cheliped may be rapped against the ground in a flexed position.

Burkenroad (1947b) observed a drumming sound produced by males vibrating their large cheliped just outside the burrow at night, or in daytime just after waving and retreating into the burrow. Pearse (1914) was never able to observe copulation in the field following display, but did observe five matings of captive pairs in the laboratory. Females mated in the "hard shell" condition.

Color changes in *U. pugilator* have been investigated extensively in recent years. Carlson (1937) contended that the chromatophores respond to humoral control by the sinus gland in the eyestalks. Brown and Sandeen (1948) and Brown and Webb (1948) showed that there is a rhythmic secretion of hormone which operates to disperse the black and white pigments in the day and concentrate these at night. Superimposed on these responses are responses to background color, to total illumination, and to temperature, such that both pigments tend to disperse as intensity of illumination increases; but black pigment tends to concentrate as temperature increases above or decreases below about 15° C., and white pigment tends to disperse as temperature is increased above or decreased below about 20° C. Such lightening or darkening has been recorded in the field by a number of observers. Brown (1950) extended Carlson's work on red chromatophores, giving evidence for the activating principles and their daily rhythmicity. Further experiments with black chromatophores (Webb, Bennett, and Brown, 1954) showed that the diurnal rhythmic darkening and lightening are independent of structures in the eyestalks and that a substance which concentrates black pigment participates in regulation of the chromatophore system. Guyselman (1953) described a series of five color changes or stages which occur during the premolt period of normal animals. He found (as suggested earlier by Abramowitz and Abramowitz, 1940) that the sinus gland-X organ complex plays a role in regulation of metabolism of water and inorganic constituents. Evidence of a diurnal rhythm of water uptake was presented. Fingerman (1956) showed that even in the Gulf of Mexico, where tides are daily, the persistent rhythmic color changes re-

main scheduled as they are in crabs living where tides are semidiurnal, but (1957) that for a given local area the phase may be slightly altered according to the time that the burrows are uncovered by a receding tide.

Extending their investigations on rhythmicity, Brown, Webb, Bennett, and Sandeen (1955) showed that oxygen consumption in both *U. pugilator* and *U. pugnax* shows apparent persistent trends related to solar and lunar cycles.

As a sidelight to work with eyestalkless *U. pugilator*, Brown and Jones (1949) found that removal of eyestalks from adult females resulted in a period of rapid ovarian growth, with accompanying increase in oocyte diameter and a color change of the ovary from light pink to deep purple. Eggs produced by such animals failed to become attached to the pleopods.

The subject of intersexuality and relative growth was reopened by Darby (1935) as a result of examination of some 9,000 specimens of *U. pugilator* collected at Beaufort, N.C. Among these, 12 females were obtained with 2 fiddles, but no female was found in 1 large chela. These 12 specimens had fully widened, typically female abdomens and were always found feeding with the males in contrast to the other small-clawed females which stayed close to their holes. Darby termed these female-to-male intersexes. A male-to-female intersex; that is, a crab with a typical male abdomen and normal reproductive appendages, yet with small claws, was found only once, at Charleston, S.C. Because feeding is accomplished with the small claw, even partially symmetrical males must be handicapped in obtaining food, and it is not surprising that perfectly symmetrical adults do not, or rarely, occur. Darby, thus, refuted the arguments of Huxley and Rathbun that females with narrow abdomens were merely extremes in the normal variation curve for female abdomen growth, and supported the contention of Morgan that these were truly intersexes.

Superfamily Oxyrhyncha

Carapace more or less narrowed in front, and usually produced to form a rostrum; branchial regions considerably developed, hepatic regions small. Epistome usually large; buccal cavity quadrate, with anterior margin usually straight.

Gills almost always nine in number on each side; efferent channels opening at sides of endostome or palate. Antennules longitudinally folded (Rathbun, 1925).

Family Majidae

Chelipeds specially mobile, usually about same size as other legs with fingers straight. Second article of antenna well developed, generally fused with epistome and often with front. Orbits generally more or less incomplete. Hooked hairs almost always present. Male openings coxal (Borradaile, 1907). Palp of external maxilliped articulated either at summit or at anterointernal angle of merus (Alcock, 1895). First pleopod greatly exceeding second pleopod in length (Garth, 1958).

KEY TO SUBFAMILIES OF MAJIDAE IN THE CAROLINAS

Modified after Garth (1958)

- a. Eyes either without orbits, or with commencing orbits.
 - b. Eyes without orbits; eyestalks generally long, either nonretractile, or retractile against sides of carapace, or against acute postocular spine affording no concealment; basal (fused) antennal article extremely slender and usually long-----*Inachinae* (p. 236).
 - bb. Eyes with commencing orbits; basal (fused) antennal article not extremely slender.
 - c. Eyes lacking a postocular cup, but with tubelike housing.
 - d. Eyestalks long; orbit partially protected by a hornlike supraocular spine or eave, a strong postocular tooth, or both; body truncate in front-----*Ophthalmiinae* (p. 246).
 - dd. Eyestalks short, relatively immobile, and either concealed by a supraocular spine, or sunk in sides of rostrum; basal antennal article truncate-triangular-----*Acanthonychinae* (p. 248).
 - cc. Eyes with cupped postocular process into which eye retracts, and with a supraocular eave or spine-----*Pisinae* (p. 250).
 - aa. Eyes with complete or nearly complete orbits; basal antennal article broad, expanded to form floor to orbit-----*Mithracinae* (p. 254).

Subfamily Inachinae

Eyes without orbits; eyestalks generally long, either nonretractile, or retractile against sides of carapace, or against an acute postocular spine. Basal article of antenna extremely slender throughout its extent, and unusually long (Alcock, 1895). First pleopod not very stout, straight or curved, apically tapering, but apex most varying (hairy, spinose, naked, etc.; acute, blunt, bifid, etc.); second pleopod short (Stephensen, 1945).

KEY TO GENERA OF INACHINAE IN THE CAROLINAS

Modified after Garth (1958)

- a. Seven free abdominal segments in both sexes; rostrum double-----*Anomalothir* (p. 236).
- aa. Six free abdominal segments in male, five in female.
 - b. Rostrum double.
 - c. Interantennular spine present and conspicuous.
 - d. Spine of basal antennal article equally advanced with front-----*Euprognatha* (p. 237).
 - dd. Spine of basal antennal article not equally advanced with front-----*Batrachonotus* (p. 238).
 - cc. Interantennular spine absent or inconspicuous.-----*Collodes* (p. 239).
 - bb. Rostrum single.
 - c. Merus of outer maxilliped as broad as ischium; palp of moderate size.
 - d. Postorbital tooth large, curving around side of eye-----*Pyromaia* (p. 240).
 - dd. Postorbital tooth small, or if large not curving around side of eye-----*Anasimus* (p. 240).
 - cc. Merus of outer maxilliped often narrower than ischium; palp large and coarse.
 - d. Rostrum considerably less than postrostral length; basal antennal article often longitudinally sulcate-----*Podochela* (p. 241).
 - dd. Rostrum approaching or surpassing postrostral length; basal antennal article not longitudinally sulcate.
 - e. Carapace nodulose; a long spine at end of merus of walking legs; rostrum sparsely spined-----*Metoporphaphis* (p. 243).
 - ee. Carapace smooth; spine at end of merus of walking legs no longer than others; rostrum multispinose-----*Stenorynchus* (p. 244).

Genus *Anomalothir* Miers, 1879

Rathbun, 1925, p. 23.

Anomalothir furcillatus (Stimpson)

Figures 212, 223A

Anomalopus furcillatus Stimpson, 1871a, p. 125.

Anomalothir furcillatus: Rathbun, 1925, p. 24, text-fig. 6, pl. 8, fig. 2; pl. 9, fig. 2; pl. 206 (rev.).

Recognition characters.—Carapace much elongated, almost subcylindrical, pubescent, with regularly placed tubercles. Rostrum long, from two-thirds to 1.25 times as long as remainder of carapace, bifurcate, horns contiguous for half or more of length, slightly divergent. Eyes without orbits; pre- and post-orbital spines small, acute. Antenna visible in dorsal view, basal article narrow. Merus of maxilliped without notch at inner angle where palp inserts.

Chelipeds in adults longer than carapace; merus subcylindrical, with row of small spines below

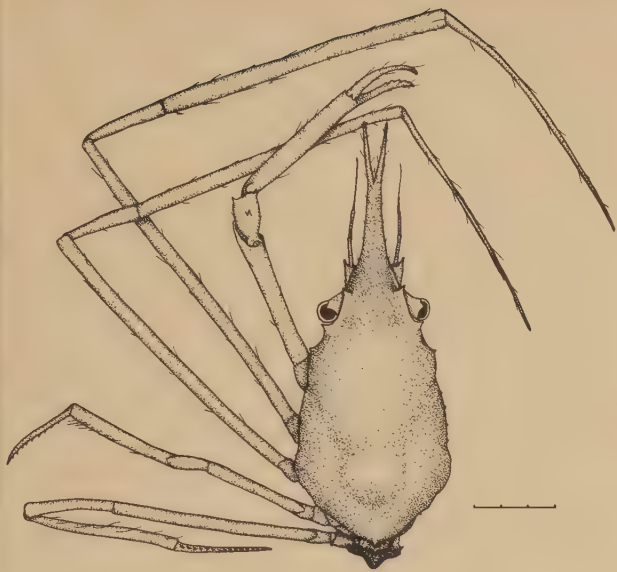


FIGURE 212.—*Anomalothir furcillatus* (Stimpson). Female in dorsal view, legs of right side not shown, 3 mm. indicated.

and less distinct row above; carpus with three spines on outer surface; palm unarmed, elongate; fingers short, stout, less gaping in male than in female. Walking legs pubescent; first two pairs long, slender; third and fourth pairs shorter, prehensile, with dactyls spinose on inner border; third pair shortest, merus with three strong hooked spines beneath, propodus and curved dactyl of about equal length; fourth pair intermediate in length, nearly straight, with propodus longer than dactyl.

Abdomen of both sexes with seven free segments.

Measurements.—Carapace: male, length including rostrum, 17 mm.; width, 6 mm. Length of rostrum, 7.5 mm. Carapace: female, length including rostrum, 20 mm.; width, 5 mm. Length of rostrum, 6 mm.

Color.—Light orange yellow; palms much deeper color (Henderson in Rathbun, 1925).

Habitat.—Rathbun (1925) listed this form from sandy, broken shell, pebbled, and rocky bottoms; 30 to 262 fathoms.

Type locality.—Off "The Samboes" [Southern Florida], 123 fathoms.

Known range.—Off Cape Lookout, N.C., through Gulf of Mexico and West Indies to Grenada.

Remarks.—Though the depth range of this species is usually beyond the 100-fathom mark, it may occur in shallower water in the Carolinas. Ovigerous females are known from the north-eastern Gulf of Mexico in March.

Genus *Euprognatha* Stimpson, 1871

Rathbun, 1925, p. 95.

Euprognatha rastellifera marthae Rathbun

Figures 213, 223B

Euprognatha rastellifera Stimpson, 1871a, p. 123.—Hay and Shore, 1918, p. 454, pl. 37, fig. 7.

Euprognatha rastellifera marthae Rathbun, 1925, p. 96, text-fig. 30, pl. 33; pl. 34, figs. 1-2; pl. 35, figs. 3-4; pl. 216 (rev.).

Recognition characters.—Carapace pyriform, granulate, a tubercle or short truncate spine on gastric and cardiac regions, each branchial region, and supraorbital margin. Rostrum short, with two small teeth on horns. Ocular peduncles short, with tubercle at emargination of cornea. Frontal teeth short, spiniform, or triangular. Postorbital projection dentiform, triangular, tapering to a slender point. Obtuse antennal spines directed obliquely forward, approximately as advanced as front; interantennular spine inclined downward, equaling or surpassing front. Sides of hepatic and pterygostomial region with a few



FIGURE 213.—*Euprognatha rastellifera marthae* Rathbun. Male in dorsal view, legs of left side not shown, 5 mm. indicated.

small spines. Sternum granulate except for concave portion between chelipeds.

Chelipeds approximately twice as long as carapace, granulate, margins spinous; hand swollen; fingers more than half length of palm, slightly gaping. Walking legs granulate, with tufts of curled setae and often small spines; first pair longest, others successively shorter.

Abdomen of males with six, females with five, free segments.

Measurements.—Carapace: male, length, 14 mm.; width, 12 mm.

Variations.—Rathbun (1925) divided the species *E. rastellifera* into a northern subspecies, *marthae* (ranging from Nantucket to southern Florida), and a southern or Caribbean subspecies, *acuta* (ranging from Cuba to Grenada and Barbados), with a region of intergradation in the Florida Keys from which *rastellifera* was originally described. The southern subspecies (*acuta*) has longer, sharper, and more slender spines than *marthae*, and a narrower, higher, and more closely and finely roughened carapace with regions more deeply separated than in the more northern forms. Likewise, the chelipeds have spines on the border of the merus well developed and legs more spinulose than in the northern forms.

Rathbun pointed out that there is considerable overlap in distribution of these subspecies, listing *acuta* from as far north as Marthas Vineyard. Such subspecific treatment seems untenable today, for such overlap of geographic range can hardly exist. No typical form was designated. I have retained the subspecific name *marthae* for the Carolinian form simply because this region lies well within the range mentioned by Rathbun, but I have not studied all of the material comparatively.

Habitat.—The species has been reported from a variety of sandy and muddy bottoms; 44 to 217 fathoms.

Type locality.—Southwest of Marthas Vineyard, Mass., lat. 40° N. long. 70°57' W., 85 fathoms.

Known range.—Off Georges Bank (lat. 40°35' N. long. 67°37' W.) to Carysfort, Fla.

Remarks.—Rathbun (1925) reported an ovigerous female off Marthas Vineyard in July, and they are known off Georges Bank in November (U.S. National Museum records).

Genus *Batrachonotus* Stimpson, 1871

Rathbun, 1925, p. 122.

Batrachonotus fragosus Stimpson

Figures 214, 223C

Batrachonotus fragosus Stimpson, 1871a, p. 122.—Rathbun, 1925, p. 123, text-fig. 48, pl. 39, figs. 1–4 (rev.).

Recognition characters.—Male. Carapace triangular, broadly expanded behind; gastric, cardiac, and branchial regions strongly protuberant, each surmounted by a stout spine or large tubercle; intestinal region with two small tubercles just above posterior margin; hepatic region angular, approximating postorbital tooth. Cervical depressions deep and broad giving carapace superior outline much like frog's back. Rostrum short, formed of rounded lobes separated by a shallow notch, scarcely projecting beyond antennular fossae, margin and supraorbital margin denticulate. Basal articles of antenna with dentate margins and a small tooth at anterior extremity. Merus of outer maxilliped broad with prominent outer and inner anterior angles. Abdomen and sternum granulate except for smooth area be-

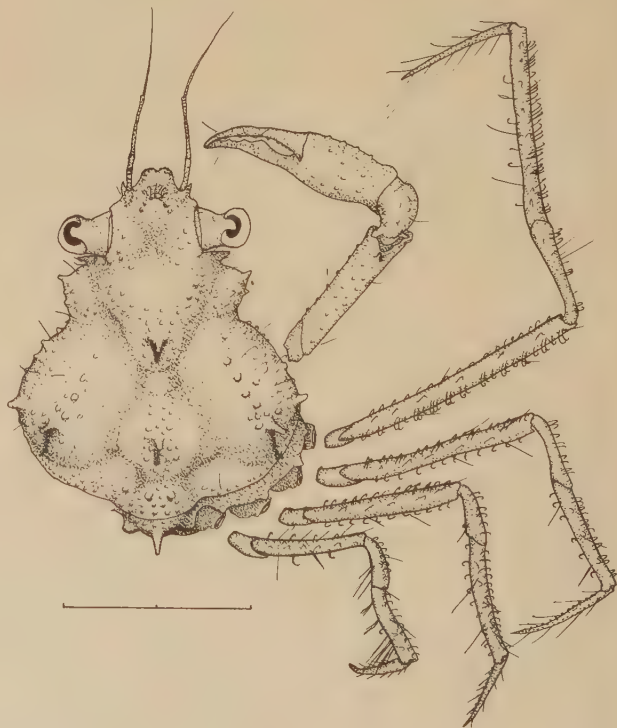


FIGURE 214.—*Batrachonotus fragosus* Stimpson. Animal in dorsal view, legs of right side shown in approximate position, legs of left side not shown, 2 mm. indicated.

tween chelipeds; abdomen with six free segments, last two fused, proximal fixed segment with a prominent median spine.

Chelipeds somewhat longer than carapace, spinulose; ischium with distal spine; hand slightly compressed; fingers nearly as long as palm, gaping nearly whole length, a large tooth in middle of immovable finger. First pair of walking legs more than twice length of second pair, posterior pairs short.

Female. Carapace narrower behind and wider in front than male, tuberculation more uniform, spines less frequent. First walking leg little longer than second, approximately 1.5 times length of carapace. Abdomen tuberculate or granulate, with five free segments, last three fused.

Measurements.—Carapace: male and female, length, 7 mm.; width, 6 mm.

Variations.—Rathbun (1925) stated that this species exhibits wide variations from the type. Some specimens have the elevated regions surmounted by a spine, some have an abdominal spine, others even lack tubercles on the elevated regions.

Habitat.—The species has been reported from mud, sand of various grades, and broken-coral and shell bottoms; shore to 75 fathoms.

Type locality.—South of Tortugas, [Fla.], lat. 24°36'40" N. long. 80°02'20" W., 16 fathoms.

Known range.—Cape Hatteras, N.C., to southern and western Florida; West Indies to Rio de Janeiro, Brazil. Ovigerous females are known from Tortugas in June (U.S. National Museum records).

Genus *Collodes* Stimpson, 1860

Rathbun, 1925, p. 105.

Collodes trispinosus Stimpson

Figures 215, 223D

Collodes trispinosus Stimpson, 1871a, p. 120.—Rathbun, 1925, p. 107, text-figs. 32a, b; pl. 36, figs. 5–6 (rev.).

Recognition characters.—Carapace ovate-triangular, covered with coarse granules except on front, anterior portion of gastric region, and about bases of spines; a single, slender, erect, capitate spine on gastric and cardiac regions, and on first abdominal segment. Rostrum short, with two minute and usually well-separated horns. Eyes of moderate length, partially retractile; postorbital tooth slender, a granule on upper

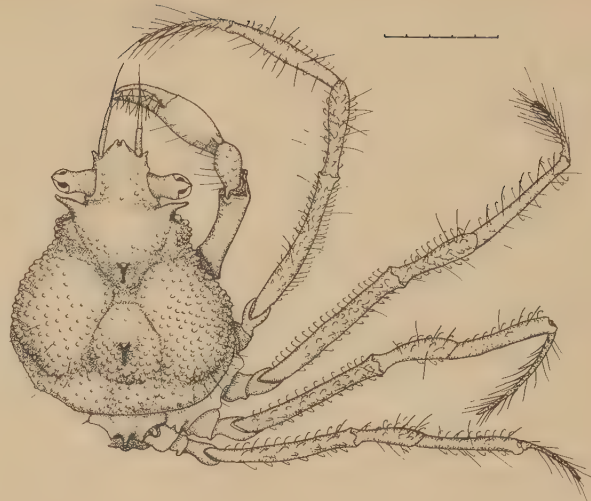


FIGURE 215.—*Collodes trispinosus* Stimpson. Male in dorsal view, legs of left side not shown, 5 mm. indicated.

orbital border. Antenna with first movable article approximately as long as rostral horns; basal article of antenna twisted, with four or five spinules on outer border and with a laminate crest on inner margin ending in a large tooth; interantennular spine short. Merus of outer maxilliped obcordate, deeply cut on distal margin, strongly produced at inner and outer angles.

Chelipeds of male moderately stout, palm thick, smooth outside; surface of carpus and margins of merus and palm spinulose; fingers widely gaping, with a triangular tooth near middle of immovable finger and a low molariform tooth near base of dactyl. Walking legs long; first two pairs variably subequal; third and fourth pairs successively shorter; dactyls as long as propodi.

Measurements.—Carapace: male, length, 14 mm., width, 12 mm.; female, length, 12 mm., width, 10 mm.

Habitat.—Rathbun (1925) reported this species from gray sands of varying coarseness, broken shell, and gravel bottoms; 4 to 82 fathoms.

Type localities.—Off the Quicksands, Carysfort Reef, and French Reef, [Fla.], 34 to 50 fathoms.

Known range.—Near Cape Hatteras, N.C., to south and west Florida near Apalachicola.

Remarks.—Rathbun (1925) reported ovigerous females from North Carolina in October, and they are known from Florida in July (U.S. National Museum records).

Genus *Pyromaia* Stimpson, 1871

Rathbun, 1925, p. 127.

Pyromaia cuspidata Stimpson

Figures 216, 223E

Pyromaia cuspidata Stimpson, 1871a, p. 110.—Hay and Shore, 1918, p. 455, pl. 38, fig. 4.—Rathbun, 1925, p. 129, text-fig. 49; pl. 41 (rev.).

Recognition characters.—Adult male. Carapace pyriform, approximately two-thirds as wide as long; regions well marked, tumid, rough, with scattered granules, sharp tubercles and spines; often six large median spines (two mesogastric, one urogastric, two cardiac, one intestinal), elsewhere one protogastric, two or three hepatic, remainder branchial. Depressions separating branchial regions from other regions somewhat pitted. Rostrum tapering to a point, trigonal; upper and lateral margins spinulose. Interantennular spine acute, triangular, pointing downward and forward. Orbits large, open; supraorbital spine almost erect, directed slightly outward and forward; postorbital tooth large, curved around end of eye; anterior margin fringed with hair. Basal article of antenna long, with terminal spine, a larger spine at middle of inner margin and a small one at middle of outer margin followed by row of tubercles or spinules. A tubercle at angle of buccal cavity. Outer maxilliped spinulose, a longitudinal depression on ischium, merus cordate.

Limbs covered with short fur, surface underneath roughened with sharp granules or spines;

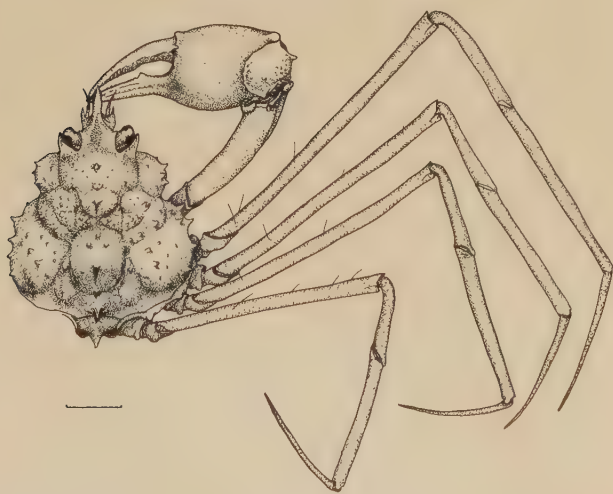


FIGURE 216.—*Pyromaia cuspidata* Stimpson. Male in dorsal view, legs of left side not shown, 10 mm. indicated.

merus of cheliped armed on margins, terminal spine of upper margin longest; upper margin of carpus spinulose with a few spines on outer surface; hand inflated, fingers bare, grooved, slightly agape at base. Walking legs spinulose; meri with distal spine; first legs longest, remainder successively shorter.

First abdominal segment long, with an acute backward-pointing spine; six free segments, last two fused.

Adult female. Limbs almost bare; chelipeds not much stronger than walking legs, dactyl longer than palm; legs shorter than in male. Five free abdominal segments, last three fused.

Measurements.—Carapace: male, length, 41 mm.; width, 32 mm.

Variations.—The young have pubescence resembling that in females, the postorbital tooth smaller than in adults, slender and directed outward in small specimens (7.5 mm. long), directed outward and forward in somewhat larger forms.

Color.—Immature individuals brown, legs with lighter crossbands.

Habitat.—This species has been taken on gray mud, sand, pebble, and broken-coral bottoms; 15 to 300 fathoms.

Type localities.—Off Sand Key, 82 fathoms; Alligator Reef, 88 fathoms; the Samboes, 93 and 121 fathoms; southwest of Sand Key, 125 fathoms [Florida].

Known range.—Off Cape Lookout, N.C., to west Florida; Yucatan Channel; Cuba.

Remarks.—U.S. National Museum records show ovigerous females off Florida in February and July.

Genus *Anasimus* Milne Edwards, 1880

Rathbun, 1925, p. 64.

Anasimus latus Rathbun

Figures 217, 223F

Anasimus latus Rathbun, 1894, p. 58.—1925, p. 65, pl. 214 (rev.).

Recognition characters.—Carapace broadly ovate, elevated on median line, posterior half semicircular, anterior half broadly triangular, surface covered with unequal granules. Carapace with median row of spines, two gastric (posterior one larger), one large cardiac, one small backward-pointing intestinal, and a long acuminate backward-projecting spine at distal end of first

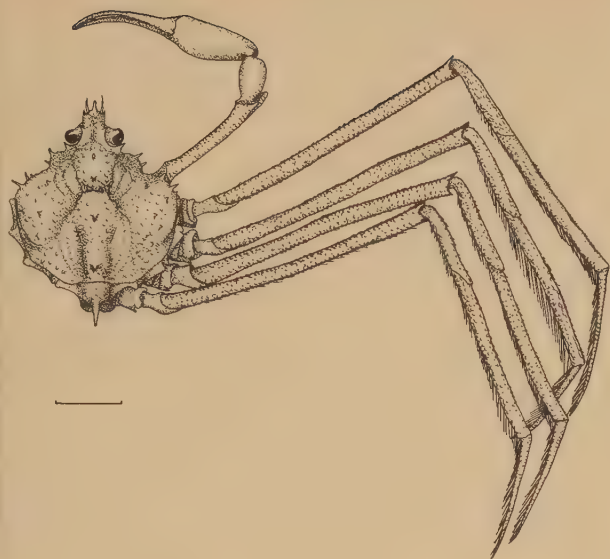


FIGURE 217.—*Anasimus latus* Rathbun. Male in dorsal view, legs of left side not shown, 10 mm. indicated.

abdominal segment; anterior gastric spine one of transverse row of about five; branchial region with three small spines or tubercles in triangular arrangement. Three anterolateral spines, one hepatic and two branchial above base of cheliped. Rostrum short, medially carinate, broadly triangular at base, ending in short, sharp, upturned spine. Eyes large; prominent supraorbital spines separated by depression, postorbital spines long, exceeding eye in large specimens. Antenna short, slightly exceeding rostrum, basal article with terminal spine and a stout spine pointing downward and forward in front of eye. Pterygostomial region with row of spines and spinules continued to antennal segment including long spine at angle of buccal cavity. Sternum of male coarsely granulate.

Chelipeds of male more than twice length of carapace, granulate; merus cylindrical; palm swollen, shorter than fingers; fingers slender, curved inward, gaping at base only, finely and evenly toothed except for larger basal tooth on dactyl. Female with chelipeds a little longer than carapace but smaller than in male, fingers not gaping. Walking legs long, slender, cylindrical, roughened, except on dactyl, with numerous short, stout, appressed spinules; propodi and dactyls with double fringe of hair.

Abdomen of male with six, female with five, free segments; female with median tubercle on third and fourth segments.

Measurements.—Carapace: male, length, 26 mm., width, 24 mm. Length of cheliped, 58 mm., of first walking leg, 106 mm.

Variations.—The adults are relatively broader than the young whose rostrum and dorsal spines are longer. The postorbital spines are very small, pointing directly outward, and with little more than a tubercle in specimens 9 mm. long or less.

Color.—Recently preserved specimens show dark reddish or brown rings on the legs (Holthuis, 1959).

Habitat.—This form has been taken from coarse sand, coral, coral sand, and mud and shell bottom; 26 to 88 fathoms.

Type locality.—Gulf of Mexico, east of Delta of Mississippi River, lat. $29^{\circ}14'30''$ N. long $88^{\circ}09'30''$ W., 68 fathoms.

Known range.—Off Cape Lookout, N.C., to off Tabasco, Mexico (Hildebrand, 1954); west of Trinidad, and off Surinam (Holthuis, 1959).

Remarks.—Ovigerous females have been reported from southern Florida and the northern Gulf of Mexico in all seasons of the year, from North Carolina in June (Rathbun, 1925, and U.S. National Museum records), and Surinam from April to August (Holthuis, 1959).

Genus *Podochela* Stimpson, 1860

Rathbun, 1925, p. 31.

KEY TO SPECIES IN THE CAROLINAS

- a. Rostrum broad, rounded in front.
 - b. Dactyls of last three pairs of legs less than one-half length of propodus; pterygostomial region bearing a broad, spinelike projection.....*riisei* (p. 241).
 - bb. Dactyls of last three pairs of legs one-half or more length of propodus; pterygostomial region bearing a long thin lamina.....*sidneyi* (p. 242).
 - aa. Rostrum long, spiniform.....*gracilipes* (p. 243).

Podochela riisei Stimpson

Figures 218, 223G

Podochela riisei Stimpson, 1860a, p. 196, pl. 2, fig. 6.—Hay and Shore, 1918, p. 453, pl. 37, fig. 9.—Rathbun, 1925, p. 33, text figs. 9a–b; pl. 11, figs. 1–2; pl. 208, fig. 2 (rev.).

Recognition characters.—Carapace pyriform, depressed, widest near posterior margin, greatest width about two-thirds length, dorsal region uneven and with tufts of hairs. Rostrum broad,



FIGURE 218.—*Podochela riisei* Stimpson. Animal in dorsal view, legs of left side not shown, 5 mm. indicated.

rounded in front, deeply excavated below for antennules, carinate above and with a tuft of curled hairs. Orbits rounded, margins thickened and with a row of hairs. Eyestalks short and stout, cornea oblique, dorsal emargination with distal tubercle tufted. Basal article of antenna with a high crest on each margin. Sternum of male thrown into ridges radiating to bases of legs.

Chelipeds slender in both sexes, fingers in contact throughout their length (stouter and slightly agape proximally in adult males). First pair of walking legs stouter than others, about three times as long as carapace; upper surface of all legs with regularly spaced tufts of stiff curled hairs.

Abdomen of male with six, female with five, free segments.

Measurements.—Carapace: male, length, 21 mm., width, 16 mm.; female, length, 23 mm., width, 20 mm.

Variations.—The rostrum is variable in shape and length. Margins of the basal antennal articles are thick in old individuals but may be thin in younger ones. Sternal segments of males usually have rounded surfaces but are sometimes flattened.

Color.—Overall color light brown; legs lighter, grading to almost off white or pale yellow; chelae and chelipeds nearly white to almost transparent; carapace darker on lateral aspects of urogastric and cardiac regions, as well as at posterolateral portions of metabranchial regions. Wass (1955) reported brick red specimens.

Habitat.—Has been taken from among hydroids on pilings at Beaufort, N.C., and in rocky areas in northwestern Florida (Wass, 1955); shallow water to 30 fathoms.

Type locality.—Island of St. Thomas, [West Indies].

Known range.—North Carolina to Campeche, Mexico; through West Indies to St. Thomas; Rio de Janeiro and south of Pernambuco, Brazil; Bermuda.

Remarks.—Ovigerous females have been taken in North Carolina in September. They have been taken in Florida from June to August and from November to February (U.S. National Museum records).

Podochela sidneyi Rathbun

Figures 219, 223H

Podochela sidneyi Rathbun, 1924, p. 1.—Rathbun, 1925, p. 39, text-fig. 9c, pls. 12–13 (rev.).

Recognition characters.—Closely resembling *Podochela riisei*. Rostrum narrower at base. Pterygostomian region bearing a long thin lamina either subtriangular or produced downward in a lobe. Sternal segments flat with sharp cristate margins.

Chelipeds of adult male less inflated than in *P. riisei*, proximal gape narrower, teeth on cutting edges more numerous and uniform in size. Walk-

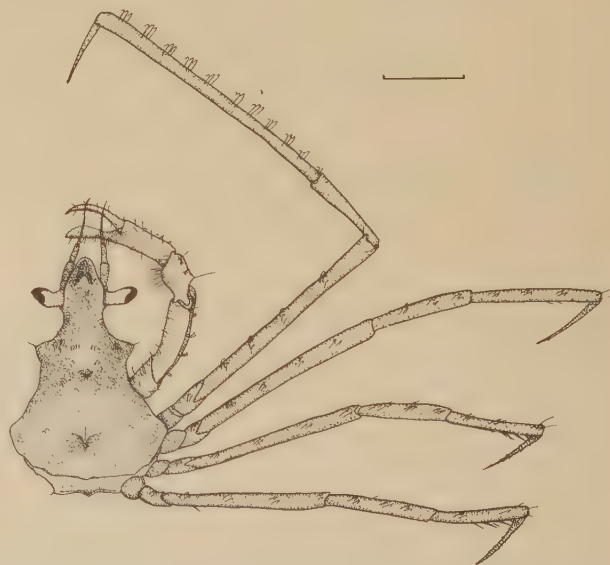


FIGURE 219.—*Podochela sidneyi* Rathbun. Animal in dorsal view, legs of left side not shown, 5 mm. indicated.

ing legs longer than in *P. riisei*; first pair of walking legs 3 or more times as long as carapace; dactyls of last three pairs less curved, longer and relatively more slender than in *P. riisei*; dactyl of second leg up to one-half length of propodus, of third leg to two-thirds, and of fourth leg to three-fourths length of propodus.

Abdomen of male with six, female with five, free segments.

Measurements.—Carapace: male holotype, length, 14 mm., width, 11 mm.

Habitat.—Shallow water to 102 fathoms.

Type locality.—Off Cape Hatteras, N.C., 49 fathoms.

Known range.—Off Cape Hatteras, N.C., to Port Aransas, Tex.; northwestern Cuba; Yucatan Channel.

Remarks.—Hildebrand (1954) reported the carapace of this species as decorated with hydroids and ascidians.

Podochela gracilipes Stimpson

Figures 220, 223I

Podochela gracilipes Stimpson, 1871a, p. 126.—Hay and Shore, 1918, p. 454, pl. 37, fig. 6.—Rathbun, 1925, p. 47, text-fig. 12, pl. 17 (rev.).

Recognition characters.—Carapace narrow, pyriform, depressed; constricted behind orbits; with rounded protuberance on cardiac region and two smaller median protuberances on gastric regions. Rostrum long, spiniform, hairy, unarmed. Sternum of males with thick blunt spine at base of cheliped. Crests on basal article of antenna less pronounced than in *P. riisei*, article long, narrow posteriorly, with a diagonal ventral ridge merging with terminal spine distally.

Chelipeds in male stout, inflated, fingers widely agape to near tip, large tooth near base of dactyl. Chelipeds slender in female. Walking legs slender, first pair three times length of carapace; dactyls long, nearly straight, one-third length of propodus; propodi of last three pairs thickened distally; dactyls slightly scythe-shaped, two-fifths length of propodus on second pair, one-half length on third, and two-thirds length of propodus on fourth pair.

Abdomen of male with six, female with five, free segments.

Measurements.—Carapace: male, length, 13 mm., width, 9 mm.; ovigerous females, length, 9 mm., width, 6 mm.



FIGURE 220.—*Podochela gracilipes* Stimpson. Animal in dorsal view, legs of left side not shown, 5 mm. indicated.

Habitat.—Eighteen to 120 fathoms.

Type localities.—West of Tortugas, off Pacific and Carysfort Reefs, [Fla.], 36 to 60 fathoms.

Known range.—Off Cape Lookout, N.C., to Gulf of Mexico; Caribbean Sea to Columbia and Barbados; Cabo Frio, Brazil.

Remarks.—Ovigerous females are known in December from North Carolina.

Genus *Metoporphaphis* Stimpson, 1860

Rathbun, 1925, p. 19.

Metoporphaphis calcarata (Say)

Figures 221, 223J

Leptopodia calcarata Say, 1818, p. 455.

Metoporphaphis calcaratus: Hay and Shore, 1918, p. 454, pl. 37, fig. 5.

Metoporphaphis calcarata: Rathbun, 1925, p. 21, text-fig. 5, pls. 6-7 (rev.).

Recognition characters.—Carapace triangular, longer than broad, uneven, nodulose with each nodule surmounted by a tubercle and this in turn usually with a pencil of soft, hooked hairs. Rostrum as long as or longer than carapace, subcylindrical, tapering to a point, often armed with four or five slender spines projecting outward alternately from opposite sides of lower surface, and with distal pair so close to tip as to give tip bi- or tri-spinose appearance. Eyes protuberant, peduncles terminating in superior spinule project-

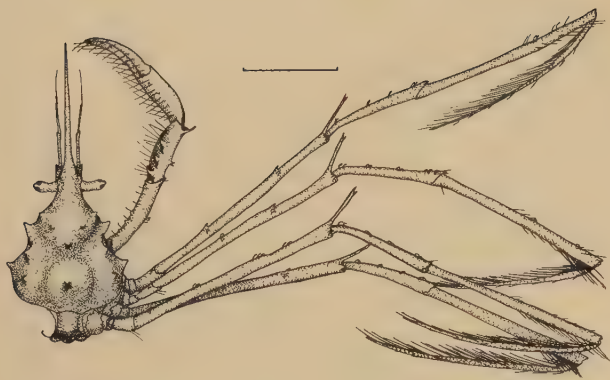


FIGURE 221.—*Metoporphaphis calcarata* (Say). Animal in dorsal view, legs of left side not shown, 10 mm. indicated.

ing beyond cornea. Basal antennal article with spine below at midpoint of length, another at outer distal angle, and a spinule at end of next two articles.

Chelipeds of moderate length, twisted, stout in male and less than half as long as first walking legs, margin of lower (really inner) surface armed with sharp spines; merus with sharp terminal spine; carpus with two sharp dorsal spines, one near each extremity of upper surface; hand broad, inflated; fingers about as long as palm, bent medially. Female with chelipeds feebler, palm shorter, fingers longer and more gaping. Walking legs slender, articles cylindrical but somewhat crooked; meri with one conspicuous spine and two smaller spines at extremity; dactyls longer than propodi, fringed with hair.

Male with six, female with five, free abdominal segments.

Measurements.—Carapace: female, length (including rostrum), 21 mm., width, 10 mm. Length of rostrum, 11 mm.

Color.—Dirty gray to lemon yellow.

Habitat.—Often found among hydroids near Morehead City, N.C., and also taken in dredges in Bogue Sound nearby; shallow water to 49 fathoms.

Type locality.—Bay of Charleston, S.C.

Known range.—Off Cape Hatteras, N.C., to Rio de Janeiro, Brazil.

Remarks.—Ovigerous females have been taken off South Carolina in August, and in Florida in March and August (Wass, 1955). Wass also noted

that this species can remain suspended in water by "rhythmic waving of its long, setae-lined legs."

Genus *Stenorhynchus* Lamarck, 1818

Rathbun, 1925, p. 13.

Stenorhynchus seticornis (Herbst). Arrow crab

Figures 222, 223K

Cancer seticornis Herbst, 1788, p. 229, pl. 16, fig. 91 (see Rathbun, 1925).

Stenorhynchus sagittarius: Hay and Shore, 1918, p. 455, pl. 37, fig. 8.

Stenorhynchus seticornis: Rathbun, 1925, p. 13, text-fig. 3, pls. 2-3 (rev.).—Monod, 1956, p. 567, figs. 838-839.

Recognition characters.—Carapace smooth, triangular, longer than broad, diminishing in width to level of eyes and thence produced into a slender, horizontal, flattened, laterally spinuliferous rostrum varying from slightly longer to 2.5 times as long as carapace; rostral tip acuminate. Orbits not defined; postorbital spine small, occasionally bifid. Eyes short, not retractile. Basal article of antenna slender, with strong spine at middle directed downward and forward.

Legs extremely long and slender, composed of cylindrical articles, finely spinulose and bearing in addition two rows of spines on merus, two or three spines on carpus, and several terminal spines on these articles. Chelipeds slender, cylindrical; hand weak; palm of male cheliped from 2.5 to

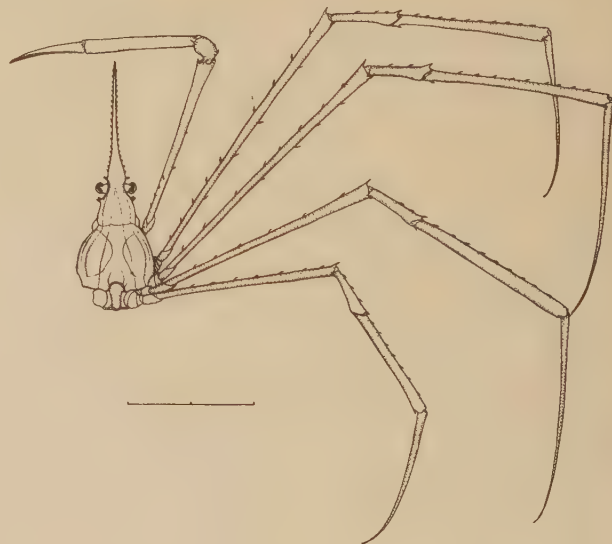


FIGURE 222.—*Stenorhynchus seticornis* (Herbst). Animal in dorsal view, legs of left side not shown, 30 mm. indicated.

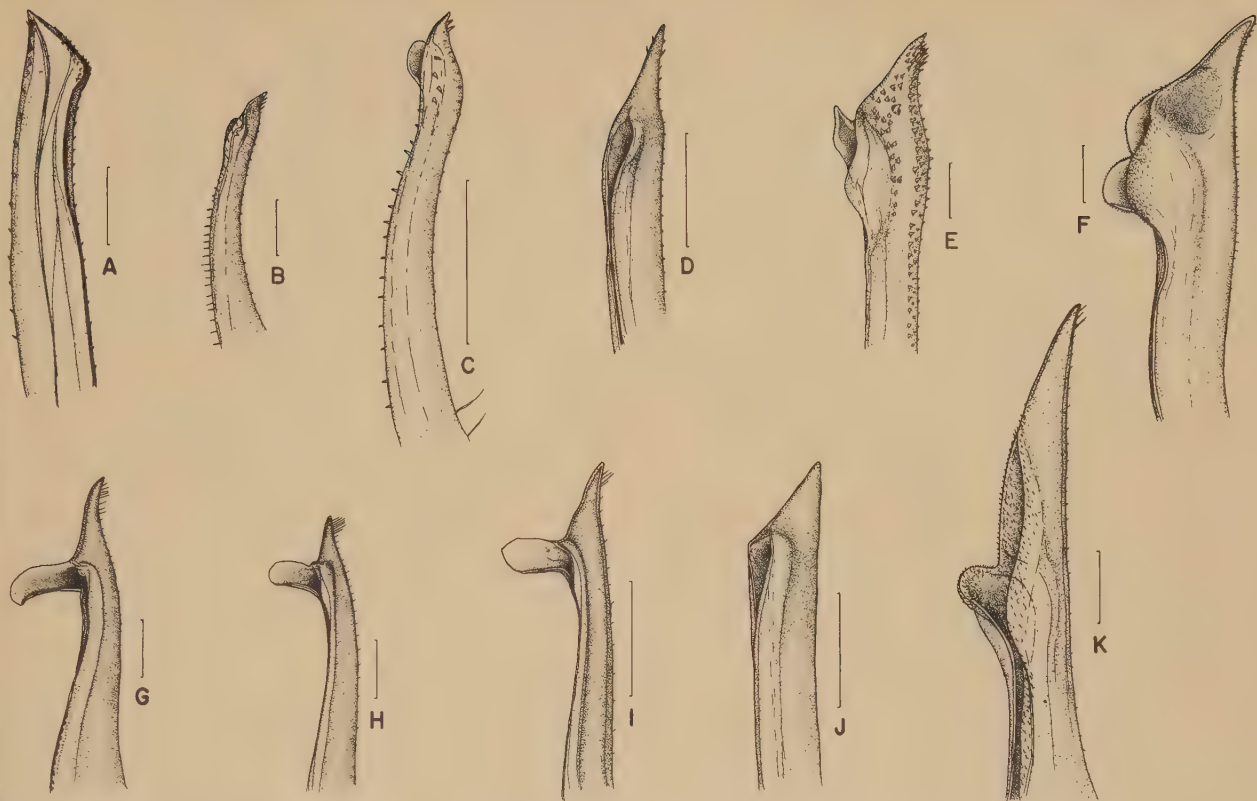


FIGURE 223.—Subfamily Inachinae, tips of right first pleopods of males; A, *Anomalothir furcillatus* (Stimpson), abdominal view; B, *Euprognatha rastellifera marthae* Rathbun, sternal view; C, *Batrachonotus fragosus* Stimpson, sternal view; D, *Collodes trispinosus* Stimpson, sternal view; E, *Pyromaia cuspidata* Stimpson, sternal view; F, *Anasimus latus* Rathbun, sternal view; G, *Podochela riisei* Stimpson, sternal view; H, *Podochela sidneyi* Rathbun, sternal view; I, *Podochela gracilipes* Stimpson, sternal view; J, *Metoporphaphis calcarata* (Say), sternal view; K, *Stenorynchus seticornis* (Herbst), sternal view; 0.33 mm. indicated.

4 times as long as dactyl. First pair of walking legs from 8 to 9 times as long as postrostral portion of carapace; second, third, and fourth legs successively shorter; dactyls on each pair longer than propodi.

Abdomen in male with six, female with five, free segments.

Measurements.—Carapace: male, length including rostrum, 57 mm.; width, 13 mm. Length of rostrum, 41 mm.

Variations.—There is great variation in length of rostrum, relative length of palm and fingers, and length of legs. In old individuals the rostrum, chelipeds, and legs are pubescent.

Color.—Body ground color gray, banded dorsally with stripes of light and dark brown or black converging anteriorly as a nested series of inverted V's; one dark pair of stripes continuing united on dorsal side and another more lateral

pair of like color on ventral side of rostrum. Legs reddish brown, joints darker; fingers of chelipeds bluish purple.

Rathbun (1925) summarized other color observations. The general pattern is as above, with ground color creamy white, buff, or light orange vermillion; stripes white, chestnut, brown, or black; legs reddish with bright red spots at joints; chelae purple or mauve; spines on legs and rostrum orange or red; eyes maroon.

Habitat.—This form has been dredged or trawled from a variety of bottoms—rock, coral rock, pebbles, sand, or sand mixed with broken shell; also, it has been taken from wharf pilings and rock jetties. Near surface to 814 fathoms.

Type locality.—Guadeloupe (Holthuis, 1959).

Known range.—North Carolina to Rio de Janeiro, Brazil; Bermuda; eastern Atlantic from Madeira and Canary Islands to Angola.

Remarks.—Though this species has a tremendous recorded range in depth, it is usually found well inside the 100-fathom mark. On September 6, 1953, an ovigerous female was collected from wharf pilings in Bogue Sound near Bogue Inlet, N.C.

Otherwise, ovigerous females are known or have been reported in the western Atlantic from February in the Gulf of Darien, throughout spring and summer in North and Middle America, and northern South America, to November off the Amazon River (U.S. National Museum records; Hildebrand, 1954; Holthuis, 1959; Rathbun, 1925).

Subfamily Ophthalmiinae

Orbit consisting, if complete, of a supraocular eave and a postocular spine; intercalated spine lacking . . . [but] . . . longer spinous outgrowths on supraocular eave and on postocular spine for most part present. Shape of body elongate, somewhat truncate in front, often provided behind with a median spine or outgrowth (Balss, 1929).

KEY TO GENERA OF OPHTHALMIINAE IN THE CAROLINAS

Modified after Garth (1958)

- a. Eyes furnished with projecting and tubular commencing orbits.....*Pitho* (p. 246).
- aa. Orbit completely unprotected below; eyes protected above by a lamellate projection consisting of supraocular eave and an outgrowth of hepatic region
Tyche (p. 247).

Genus *Pitho* Bell, 1835

Garth, 1958, p. 162.

Pitho lherminieri (Schramm)

Figures 224, 233A

Othonia lherminieri Schramm, in Desbonne and Schramm, 1867, p. 20.

Pitho lherminieri: Hay and Shore, 1918, p. 459, pl. 38, fig. 8.—Rathbun, 1925, p. 362, text-fig. 117b, pl. 128, figs. 1–2; pl. 129, figs. 1–2; pl. 252, fig. 2 (rev.).

Recognition characters.—Carapace as broad as long in adult males, longer than broad in other individuals, narrow behind in males, broader in females, roughened with tubercles of different sizes, and adorned with scattered hooked hairs. Frontal teeth forming rostrum more advanced than orbital angles. Anterolateral margins armed with five strong teeth, exclusive of postorbital tooth; first tooth largest, second and third sub-



FIGURE 224.—*Pitho lherminieri* (Schramm). Male in dorsal view, legs of left side not shown, 5 mm. indicated.

equal, fourth and fifth much smaller, second occasionally bilobed. Orbits small, tubular, deep. Antenna short, with stiff hairs on borders; basal article lamellate, forming floor of orbit; second article flat, short, and broad; third article smaller, flattened.

Chelipeds of adult male from 1.5 times to nearly twice length of body; merus subcylindrical; carpus and hand more or less compressed and distinctly angled along margins; fingers of adult male hollowed into spoon shape, touching only at extremity. In female and young male, fingers short and weak, evenly dentate, with margins in contact.

Abdomen of both sexes with seven free segments.

Measurements.—Carapace: male, length, 26 mm., width, 24 mm.; female, length, 18 mm., width, 17 mm.

Variations.—In females and young males the carapace is more tuberculate than in old males, the lateral teeth are sharper, and the last two teeth are more prominent than in mature males.

Color.—Dirty brownish yellow (Desbonne in Rathbun, 1925).

Habitat.—This species has been found on a variety of bottoms including mud, sand, shell-sand, shell, rock and coral, and grass (Rathbun,

1925). One-half to 28 fathoms, rarely to 120 fathoms.

Type locality.—Guadeloupe, in cavities of the keys.

Known range.—Off Beaufort Inlet, N.C., to west Florida; Vera Cruz, Mexico; West Indies to Islet of São Sebastião, São Paulo, Brazil.

Remarks.—Ovigerous females are known from May to November in the Bahamas and Florida, and in December from Brazil (Rathbun, 1925, and U.S. National Museum records).

Genus *Tyche* Bell, 1835

Garth, 1958, p. 172.

Tyche emarginata White

Figures 225, 226, 233B

Tyche emarginata White, 1847a, p. 206.—Hay and Shore, 1918, p. 461, pl. 39, fig. 4.—Rathbun, 1925, p. 508, pl. 272; pl. 273, figs. 7-12 (rev.).—Garth, 1946, pp. 406-408, text-fig. 1.

Recognition characters.—Carapace oblong-oval, flattened, with lamellate expansions in front covering ocular peduncles, and another prolonged and bilobed behind, stout hooked hairs on rostrum and prominent elevations. Front wide, with four long horns, lateral horns forming anterior angles of orbit, divergent, longer and more elevated than median rostral horns. Ocular peduncles entirely uncovered below. Gastric region swollen, with

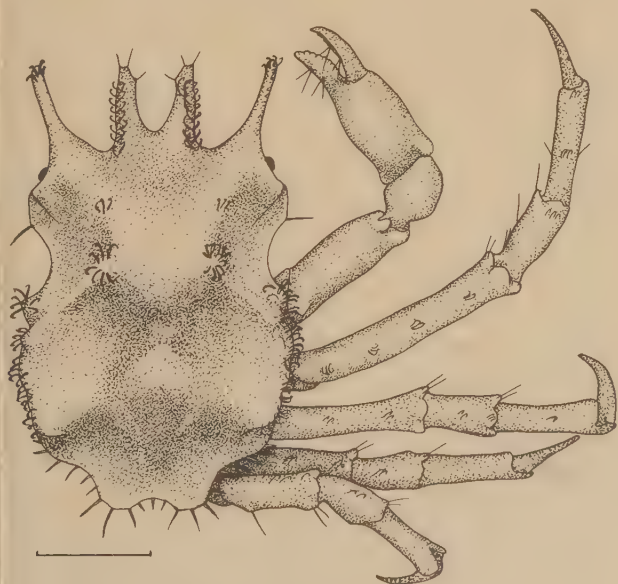


FIGURE 225.—*Tyche emarginata* White. Male in dorsal view, legs of left side not shown, 5 mm. indicated.



FIGURE 226.—*Tyche emarginata* White. Left outer maxilliped (after Garth, 1946).

three low tubercles, two anterior, and a third posterior and median; cardiac region depressed, with three small tubercles. Lateral borders straight and nearly parallel at hepatic regions, rounded at branchial regions. Dorsal surface of hepatic region concave; branchial region with large tubercle on anterior lobe, and a prominent tuberculate crest above lateral margin. Exopodite of third maxilliped with basal protuberance recurving to cover base of ischium, merus inserting deeply into outer distal portion of ischium by similar but less developed process, inner margin of ischium strongly dentate.

Chelipeds of male more than twice length of postorbital part of carapace; palms somewhat dilated and compressed; fingers gaping at base, dentate throughout length. Walking legs ornamented with stout hooked hairs; dactyls spinulose on middle third, spinules increasing in size distally.

Abdomen of both sexes with seven free segments.

Measurements.—Carapace: female, length, 35 mm.; width, 21 mm.

Color.—Generally yellowish gray; carapace greenish above, with two triangular white spots; blackish above base of legs (various authors).

Habitat.—The species has been reported from rocky or coarse shell bottoms (Rathbun, 1925); a few feet to 20 fathoms.

Type locality.—West Indies.

Known range.—Off Beaufort Inlet, N.C.; through Bahamas to west coast of Florida; Cape São Roque, Rio Grande do Norte, Brazil.

Remarks.—Garth (1946) gave a detailed comparison of this species with its Pacific counterpart, *T. lamellifrons*.

Subfamily Acanthonychinae

Eyes without true orbits; eyestalks very short or sometimes obsolescent, either concealed beneath an anteriorly produced supraocular spine, or sunk in sides of a huge beaklike rostrum; a postocular spine or process sometimes present, but not excavated for reception of retracted eye. Basal antennal article elongate but truncate-triangular. External maxillipeds with merus as broad as ischium. Dactyls of walking legs prehensile or subchelate; last three pairs of legs often disproportionately short compared with [first] pair (Alcock, 1895). Postocular spine not cupped (except in *Sphenocarcinus*); rostrum either simple or two-spined; palp on third maxilliped arising from anterointernal angle of merus (Rathbun, 1925). First pleopod medium stout, apex most varying (hammer-shaped; divided into three or four lobes; etc.); second pleopod short (Stephensen, 1945).

KEY TO GENERA OF ACANTHONYCHINAE IN THE CAROLINAS

- a. Rostrum double; seven free abdominal segments in both sexes.....*Sphenocarcinus* (p. 248).
- aa. Rostrum single or secondarily bifurcate; six free abdominal segments in male, five in female
Epiattus (p. 249).

Genus *Sphenocarcinus* Milne Edwards, 1878

Garth, 1958, p. 217.

Sphenocarcinus corrosus Milne Edwards

Figures 227, 233C

Sphenocarcinus corrosus Milne Edwards, 1875, pl. 17, figs. 5-5c.—Hay and Shore, 1918, p. 460, pl. 39, fig. 1.—Rathbun, 1925, p. 187, text-fig. 73, pl. 62; pl. 223, figs. 3-5 (rev.).

Recognition characters.—Carapace subpentagonal, broad behind, anterolateral margin concave,

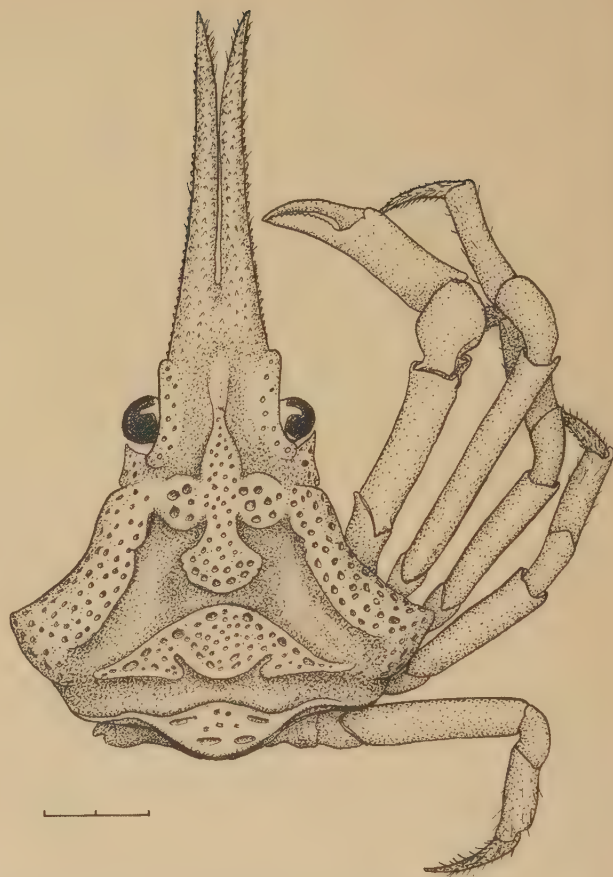


FIGURE 227.—*Sphenocarcinus corrosus* Milne Edwards. Male in dorsal view, legs of left side not shown, 2 mm. indicated.

posterolateral margin convex. Dorsal surface deeply channeled, leaving symmetrical, coarsely punctuate, or eroded elevations in regular pattern as follows: a longitudinally placed, trefoil-shaped gastric, a transversely placed cardiac with two deep posterior indentations, a transversely elongate intestinal, paired laterals extending from near lateral angles to near eyes, and paired small postocular and larger supraocular elevations; margins of all elevations sharply defined with surface finely eroded. Rostrum usually longer than carapace, formed of two pointed horns contiguous to near tips, slightly divergent in old individuals. Eye deeply sunk between two low smooth excrescences. Basal antennal article truncate, antennal flagellum hidden beneath rostrum. Epistome long, narrow.

Chelipeds weak; first pair of walking legs longer than others and exceeding length of chelipeds by more than length of dactyl.

Abdomen in both sexes with seven distinct segments.

Measurements.—Carapace: male, length, 13 mm., width, 7 mm.; ovigerous female, length, 23 mm., width, 11 mm.

Variations.—Divergence of the rostral horns varies individually. In some specimens the horns are contiguous nearly to the tip, in others the horns may be divergent for half their length, and in still others there is no evidence at all of bifurcation.

Color.—Orange-red.

Habitat.—Ninety to 148 fathoms.

Type locality.—Off Barbados, 100 fathoms.

Known range.—Off Cape Lookout, N.C., to Barbados.

Remarks.—Ovigerous females have been reported from North Carolina in April (Rathbun, 1925).

Genus *Epialtus* H. Milne Edwards, 1834

Garth, 1958, p. 227.

Epialtus dilatatus Milne Edwards

Figures 228, 233D

Epialtus dilatatus Milne Edwards, 1878, p. 140, pl. 27, figs. 4-4b.—Rathbun, 1925, p. 153, text-fig. 53j, pl. 45, fig. 2 (rev.).

Recognition characters.—Small species. Carapace broad, subpentagonal, almost smooth, with hepatic and branchial projections more or less laminate. Rostrum broad, somewhat triangular, short, bilobed at tip, slightly depressed on median line dorsally with depression continued ventrally and limited by two crests uniting posteriorly in an acute angle. Eyes small; preorbital angles scarcely marked; postorbital teeth minute. Basal article of antenna triangular, movable part concealed beneath rostrum.

Chelipeds moderate in size; carpus with four longitudinal crests; hand slightly enlarged distally, upper margin blunt, defined by depression on either side; fingers short and stout. Walking legs with slight tuft of hair on lower margin of propodi.

Abdomen of male with six, female with five, free segments.

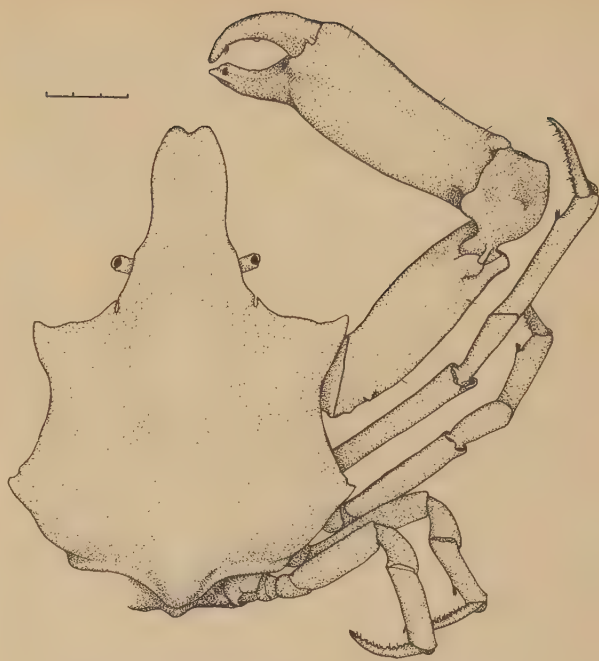


FIGURE 228.—*Epialtus dilatatus* Milne Edwards. Male in dorsal view, legs of left side not shown, 3 mm. indicated.

Measurements.—Carapace: male, length, 17 mm., width, 13 mm.; female, length, 10 mm., width, 8 mm.

Variations.—Members of the genus *Epialtus* are variable in a number of respects. The hepatic expansion may vary in shape and the rostrum may vary from triangular to suboblong in shape.

Rathbun (1925) recognized from southwestern Florida an elongate form which has a longer rostrum and slightly different lateral expansions than the typical form.

Habitat.—The species has been reported from shell reefs and coarse coral sand, and the elongate form has been found on sandy-grassy bottoms as well. Two and one-half to 12 fathoms.

Type locality.—St. Thomas.

Known range.—Off Beaufort Inlet and New River, N.C.; southwest Florida; Yucatan; Bahamas to St. Thomas.

Remarks.—Rathbun (1925) reported ovigerous females from Florida in April. They are known from North Carolina in June, and in Florida through the summer. Other records are Brazil in September, and Puerto Rico in November (U.S. National Museum records).

Subfamily Pisinae

Eyes with commencing orbits, eye retractile into sometimes large, blunt, usually isolated, cupped postocular tooth or lobe, but never to such extent as to conceal completely cornea from dorsal view; usually a prominent supraocular eave with anterior angle sometimes produced forward as a spine; eyestalks short. Basal antennal article broad, at least at base, anterior angle generally produced to form a tooth or spine. Merus of external maxilliped broader than ischium owing to expansion of anteroexternal angle, and carrying palp at anterointernal angle. Rostrum [except in *Neodoclea* among New World forms] two-spined; legs often very long (Alcock, 1895). First pleopod medium stout to slender, usually apically somewhat tapering, but apex extremely varying (blunt, acute, filiform, straight, geniculate, etc.); second pleopod short (Stephensen, 1945).

KEY TO GENERA OF PISINAE IN THE CAROLINAS

Modified after Garth (1958)

- a. Intercalated orbital spine present-----*Nibilia* (p. 251).
- aa. Intercalated orbital spine absent.
 - b. Supraocular eave and postocular process not closely approximated-----*Pelia* (p. 250).
 - bb. Supraocular eave and postocular process closely approximated-----*Libinia* (p. 251).

Genus *Pelia* Bell, 1835

Garth, 1958, p. 268.

Pelia mutica (Gibbes)

Figures 229, 233E

Pisa mutica Gibbes, 1850, p. 171.

Pelia mutica: Hay and Shore, 1918, p. 455, pl. 38, fig. 7.—Rathbun, 1925, p. 278, text-fig. 94, pl. 98, figs. 2-3 (rev.).

Recognition characters.—Small species. Carapace pyriform, greatest width approximately two-thirds greatest length, swollen, devoid of tubercles, covered with sparse pubescence, gastric and cardiac regions elevated. Rostrum well developed, two-fifths as long as remainder of carapace, formed of two more or less distally divergent horns with outer margins often parallel, a furrow on basal portion. Eyes retractile. Basal antennal article long, slender, forming incomplete floor to orbit and jutting out beyond orbital margin, usually with small tooth or spine at anteroexternal angle; antennal flagellum greatly developed.

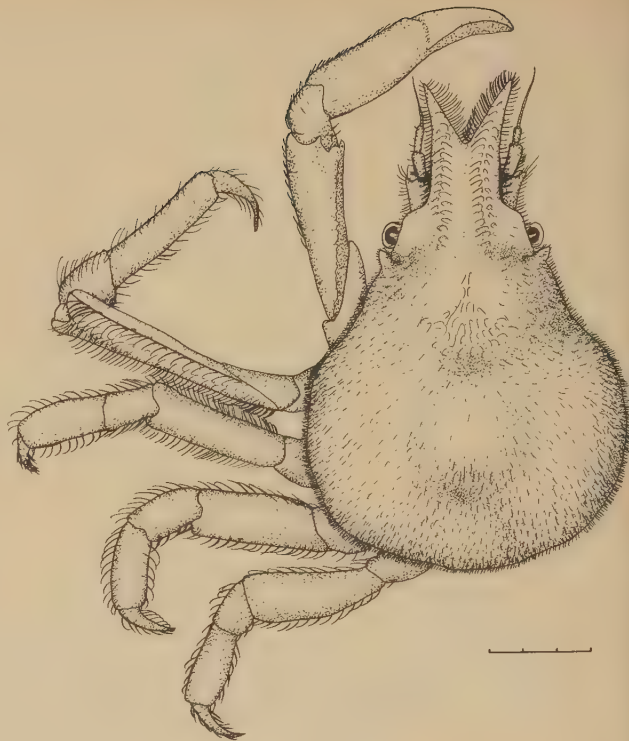


FIGURE 229.—*Pelia mutica* (Gibbes). Animal in dorsal view, legs of right side not shown, 3 mm. indicated.

Chelipeds of mature male as long as first walking legs but stouter and almost bare, weaker in females and young males; upper and inner margin of merus dentate; carpus with a longitudinal denticulate ridge; upper and lower margins of hand slightly arcuate; basal half of fingers widely agape, with denticulate margins on occludent portions and broad basal tooth of dactyl; fingers weaker and not agape in females and young males. Walking legs with marginal rows of stiff setae, meri much compressed, dactyls strongly curved.

Abdomen of both sexes with seven free segments.

Measurements.—Carapace: male, length, 13 mm., width, 9 mm.; ovigerous females, length, 5-10 mm. (Wass, 1955).

Color.—Bright red in patches on carapace and in bands on legs, spots of light red on chelipeds (Rathbun, 1925).

Habitat.—This species has been found on gravelly and shelly bottoms of bays and sounds, among hydroids, ascidians, and sponges on wharf piles, and also on shelly reefs off Beaufort Inlet,

N.C. (Pearse and Williams, 1951). Individuals are often so covered with sponge that they are difficult to recognize. Gray (1961) reported the species from *Chaetopterus* tubes. Low water to 28 fathoms.

Type locality.—Charleston Harbor, off White Point Battery, S.C.

Known range.—Buzzards Bay and Vineyard Sound, Mass., to west coast of Florida; Cuba, Puerto Rico, and St. Thomas, West Indies.

Remarks.—Ovigerous females are known from February to July in Florida, through the summer in the Carolinas, and in Massachusetts in July (Rathbun, 1925; U.S. National Museum records).

Genus *Nibilia* Milne Edwards, 1878

Rathbun, 1925, p. 289.

Nibilia antilocapra (Stimpson)

Figures 230, 233F

Pisa antilocapra Stimpson, 1871a, p. 110.

Nibilia antilocapra: Rathbun, 1925, p. 290, text-fig. 97, pls. 102, 103, and 239 (rev.).

Recognition characters.—Carapace pyriform, conspicuously spinose, much swollen, longer than wide; gastric and cardiac regions with about 18 spines of moderate size and smaller ones interspersed, largest spines surmounting summit of regions and somewhat surrounded by circle of smaller spines; other regions also well spined.

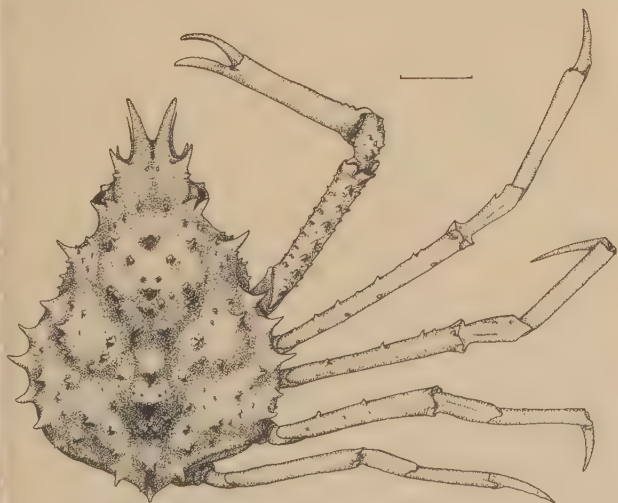


FIGURE 230.—*Nibilia antilocapra* (Stimpson). Male in dorsal view, legs of left side not shown, 10 mm. indicated.

Rostrum horizontal, undivided at base but moderately bifurcate for greater part of length, horns varying from three-fifths to four-fifths total length of rostrum. Preorbital spine ascending, slightly curved, not so advanced as base of horns; behind this a small spine on supraocular eave and a triangular (intercalated) spine or tooth on supraocular border; postocular cup terminating in a spine. Basal antennal article with a short spine just outside posterior end, behind this a tubercle in line with prominent spine at angle of buccal cavity. Maxilliped and sternum smooth.

Chelipeds of adult male longer and stouter than walking legs; merus and carpus rough with spines above and below; chelae almost cylindrical; hand nearly as long as merus, nearly smooth, a few spines near articulation with carpus; fingers agape for half of length in old males, with a well-developed tooth on dactyl in gaping part. Walking legs long, slender; merus and carpus with a few spines longitudinally arranged; dactyls long, stout, unarmed.

Measurements.—Carapace: large male, length, 120 mm., width, 82 mm.; female, approximate length, 60 mm., width, 43 mm.

Variations.—The young and half-grown are covered with short hair, but the old are nearly bare except for hairy dactyls on the walking legs.

Habitat.—The species has been reported from gray and coarse sand, broken-shell, and coral bottoms (Rathbun, 1925); 39 to 140 fathoms.

Type localities.—Florida, off Carysfort Reef, 52 and 60 fathoms; and off Alligator Reef, 118 fathoms.

Known range.—Off Cape Hatteras, N.C., to Gulf of Mexico just east of Mississippi River Delta and Gulf of Campeche; Windward Islands, West Indies.

Remarks.—Ovigerous females have been reported from St. Vincent in February and from Barbados in March (Rathbun, 1925).

Genus *Libinia* Leach, 1815

Garth, 1958, p. 322.

KEY TO SPECIES IN THE CAROLINAS

- a. Median line of carapace with about nine spines
emarginata (p. 252).
- aa. Median line of carapace with about six spines
dubia (p. 252).

Libinia emarginata Leach, 1815, p. 180, pl. 108.—Hay and Shore, 1918, p. 456, pl. 38, fig. 6.—Rathbun, 1925, p. 311, text-figs. 103-104; pls. 110-113 (rev.).

Recognition characters.—Carapace orbicular, about one-sixth longer than wide, spinose and tuberculate, with dense covering of short hairs. Larger spines arranged as follows: median row of about nine extending from near base of rostrum to posterior border consisting of four gastric, one genital, two cardiac, and two intestinal; lateral marginal spines five on each side; two subhepatic spines; two or four spines above posterior margin, aside from median spine, and about four dorsal branchial spines; spiniform tubercles scattered about among larger spines. Gastric region marked off by a deep groove. Rostrum slightly depressed, emarginate or bifid at tip; a median groove between eyes. Orbits with prominent preorbital spine, two spines beneath on basal article of antenna; one fissure above and one beneath.

Chelipeds equal, larger in male; hands granulate; fingers smooth, evenly denticulate, and about half as long as hand. Walking legs long, hairy, unarmed, often unequal and asymmetrical (result, perhaps, of injury and subsequent regeneration).

Measurements.—Carapace: male, length, 103 mm., width including spine, 94 mm.; female, length, 62 mm., width, 58 mm.

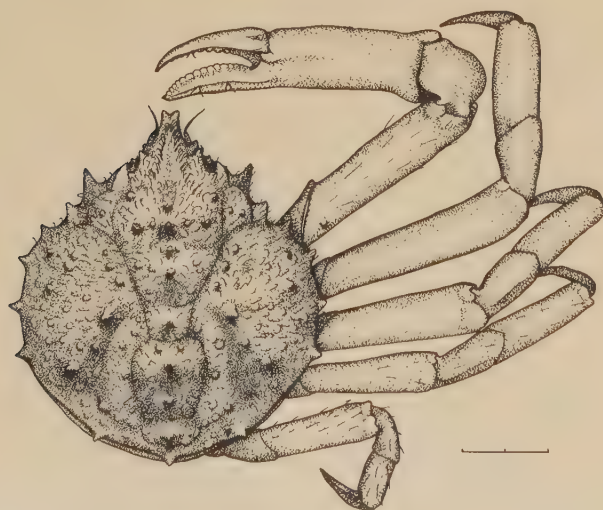


FIGURE 231.—*Libinia emarginata* Leach. Male in dorsal view, legs of left side not shown, 20 mm. indicated.

Variations.—The number of median spines in the gastric region is subject to some variation in size and number.

Color.—A brownish or dirty yellow.

Habitat.—Found on almost any kind of bottom; shore to 27, occasionally 68, fathoms.

Type locality.—Unknown.

Known range.—Windsor, Nova Scotia, to western Gulf of Mexico.

Remarks.—Hildebrand (1954) reported this species as the most common large spider crab in the western Gulf of Mexico. It was most common in July, at which time ovigerous females were observed. Another ovigerous female was taken in February. (Elsewhere ovigerous females are known from New Jersey in August (U.S. National Museum records).) Hildebrand also observed juveniles riding in the bell of scyphozoan *Stomolophus meleagris*, a habit noted by others for the young of *L. dubia*.

The young of *L. emarginata* and *L. dubia* are difficult to distinguish. Wass (1955) pointed out useful distinguishing marks. "The rostrum of *L. dubia* is much longer, forming a V; the carapace is not so wide, and there is but one spine on the intestinal region . . . whereas *L. emarginata* has two."

Gray (1957) compared gill area in this sluggish species with that of other common littoral crabs in the Carolinas and found that it had the smallest gill area per gram body weight of any studied.

Libinia dubia H. Milne Edwards. Spider crab

Figures 232, 233G

Libinia dubia H. Milne Edwards, 1834, p. 300, pl. 14bis, fig. 2.—Hay and Shore, 1918, p. 456, pl. 38, fig. 5.—Rathbun, 1925, p. 313, text-figs. 105-106; pls. 114-115; pl. 122, fig. 1 (rev.).

Recognition characters.—Similar in general characters to *L. emarginata* but with more pyriform carapace and fewer spines; median row with but six spines, two gastric, one genital, two cardiac, and one intestinal; preorbital, subhepatic, and lateral spines stronger than in *L. emarginata*, but spiniform tubercles few or wanting altogether. Rostrum slightly longer and more definitely bifid than in *L. emarginata*. Anterolateral angle of buccal frame armed with a spine.

Measurements.—Carapace: male, length, 102 mm.; width including spines, 82 mm. Most individuals smaller.

Variations.—Dorsal spines and tubercles variable in length.

Habitat.—Found on almost all types of bottom in the ocean and the saltier sounds. Occasionally, large individuals are found on Bird Shoal near Beaufort, N.C., in pools left by falling tide; frequently specimens are brought up in otter trawls. Immature individuals are often completely overgrown with sponges, hydroids, or ascidians, but the larger ones are usually almost clean. Near shore to 25 fathoms.

Type locality.—Côtes des Etats-Unis.

Known range.—Cape Cod, Mass., to southern Texas; Bahamas and Cuba.

Remarks.—This species has a geologic record extending from the upper Miocene of Virginia (Rathbun, 1935) through the Pleistocene of New



FIGURE 232.—*Libinia dubia* H. Milne Edwards. Male in dorsal view, legs of left side not shown, 10 mm. indicated.

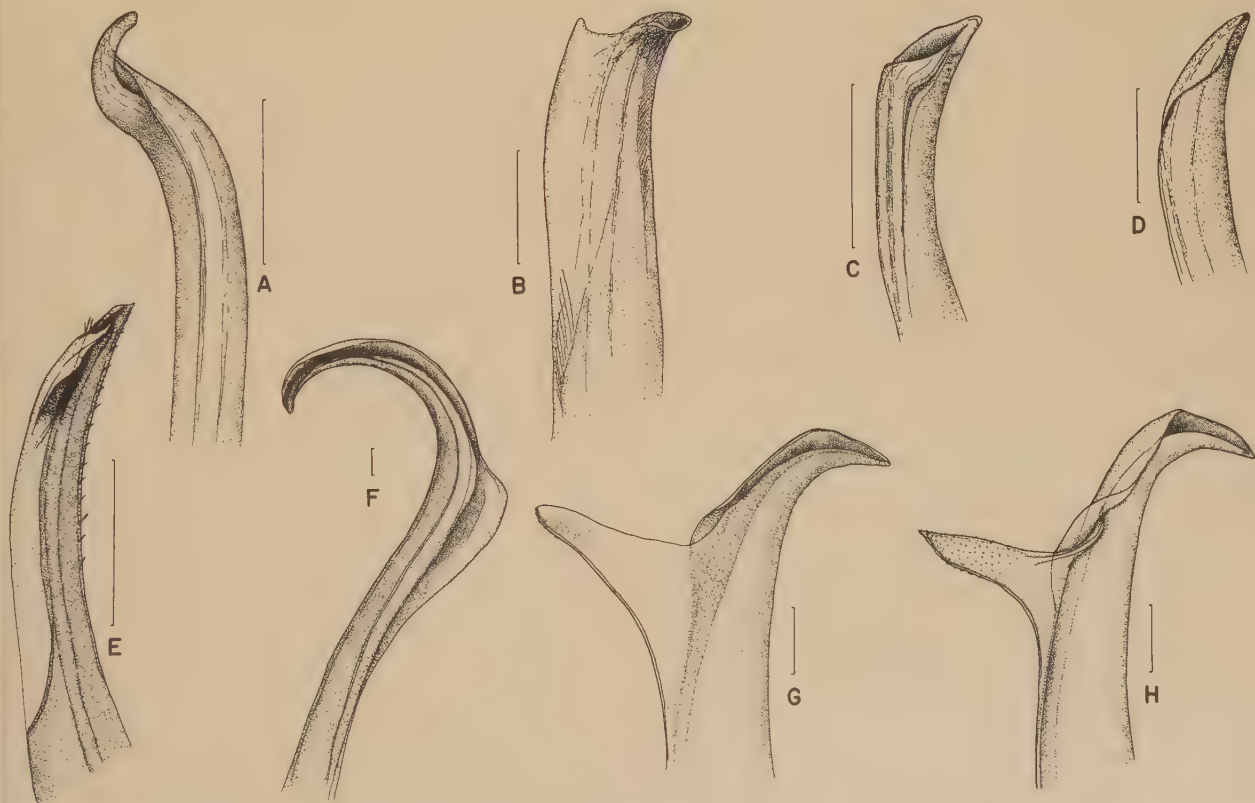


FIGURE 233.—Subfamilies Ophthalmiinae, Acanthonychinae, and Pisinae, tips of right first pleopods of males; A, *Pitho therminieri* (Schramm), abdominal view; B, *Tyche emarginata* White, lateral view; C, *Sphenocarcinus corrosus* Milne Edwards, sternal view; D, *Epialtus dilatatus* Milne Edwards, sternal view; E, *Pelia mutica* (Gibbes), sternal view; F, *Nibilia antilocapra* (Stimpson), abdominal view; G, *Libinia dubia* H. Milne Edwards, lateral view; H, *Libinia emarginata* Leach, lateral view; 0.33 mm. indicated.

Jersey (Rathbun, 1935) and Maryland (Easton, 1940).

Ovigerous females are known to occur in spring in North Carolina.

Pearse (1929), studying the survival rates of various estuarine crabs in dilutions of sea water and in air, found *L. dubia* least able to survive desiccation and dilutions of sea water. Ayers (1938), in a study of the relationship of habitat to oxygen consumption among certain estuarine crabs, found that *L. dubia* lives much of the year in relatively deep [estuarine] water where there is low oxygen content, sometimes very little. The species is correspondingly sluggish and slow. Gray (1957) showed that gill area per gram of weight in this species is small.

A peculiar association of this species with the jellyfish *Stomolophus meleagris* has been reported. The crabs have been found in the subumbrellar space and on occasion small specimens have been taken from the genital pits. Corrington (1927) found medusae with crabs between Sullivan's Island and Isle of Palms, S.C., in May, and Gutsell (1928) found the association in the vicinity of Cape Lookout, N.C., in summer and fall. The crabs were found in adult jellyfish and varied in length from 3 to 37 mm.

Pearse (1952b) reported *Octolasmis lowei* (= *mulleri*) on the gills and mouth parts, and *Chelonibia patula* on the carapace of *L. dubia* in Texas.

Subfamily Mithracinae

Carapace broadened anteriorly by outstanding, often tubular, orbits; orbits formed (1) by an arched supraocular hood, or semitubular horn, (2) by a hollowed postocular process, and (3) by a remarkable broadening, or by a prolongation, of anterior part of basal antennal article, affording complete concealment to retracted eye. Rostrum often more or less deflexed (Alcock, 1895). First pleopod like that in Pisinae; second pleopod short (Stephensen, 1945).

KEY TO GENERA OF MITHRACINAE IN THE CAROLINAS

Modified after Garth (1958)

- a. Intercalated orbital spine present (between supraorbital and postorbital spine); orbits projecting somewhat beyond general outline of carapace, but not tubular.

- b. Rostrum small; carapace ovate, usually broader than long.....*Mithrax* (p. 254).
bb. Rostrum large, usually with two strong horns; carapace broadly pyriform; basal antennal article armed with a prominent spine at anteroexternal angle.....*Microphrys* (p. 259).
aa. Intercalated orbital spine absent; orbits tubular.
b. Lateral margin of carapace armed with series of strong spines; basal antennal article very broad.....*Stenocionops* (p. 260).
bb. Lateral margin of carapace not armed with series of strong spines, but with a spine, usually strong, at lateral angle of carapace.....*Macrocoeloma* (p. 263).

Genus *Mithrax* Desmarest, 1823

Garth, 1958, p. 352.

KEY TO SPECIES IN THE CAROLINAS

(Modified from Garth, 1958, and Rathbun, 1925)

- a. Carapace roughened to greater or lesser extent by tubercles or spinules, branchial grooves wanting; intermediate orbital teeth conspicuous, pointed, or subtruncate.....(Subgenus *Mithrax*).
b. Hand armed above with spines or spinules.
c. Two spines only on basal (fused) article of antenna.....*spinosissimus* (p. 254).
cc. Three spines on basal (fused) article of antenna; carapace paved with flattened granules, concealed by short hair.....*verrucosus* (young) (p. 255).
bb. Hand not armed above with spines or spinules.
c. Carapace paved with close-set, tessellated granules.....*verrucosus* (p. 255).
cc. Carapace not paved with close-set, tessellated granules.
d. Gastric region without definite transverse row of five tubercles.....*hispidus* (p. 256).
dd. A transverse row of five tubercles across gastric region.....*pleuracanthus* (p. 257).
aa. Carapace smooth and bearing oblique branchial grooves, either strongly or weakly indicated; intermediate orbital teeth inconspicuous, tuberculiform (Subgenus *Mithraculus*).

Carapace broader than long; anterolateral margins cut into spines, or angular lobes, or spines and lobes; four anterolateral protuberances behind orbit

forceps (p. 258).

Mithrax (Mithrax) spinosissimus (Lamarck)

Figures 234, 245A

Maia spinosissima Lamarck, 1818, p. 241.

Mithrax spinosissimus: Rathbun, 1925, p. 383, pl. 135 (rev.).

Recognition characters.—Large. Carapace nearly naked, subcircular, approximately as broad as long; surface rough with short spines, those in center blunt, elsewhere sharp; cervical suture deep; hepatic and cardiac regions distinctly delimited. Rostral horns narrow, obliquely truncate and granulate at extremity, separated by a U-



FIGURE 234.—*Mithrax* (*Mithrax*) *spinosissimus* (Lamarck). Male in dorsal view, legs of left side not shown, 30 mm. indicated.

shaped notch of equal length and breadth; two stout spines at base of horns and two more behind these but farther apart; preorbital spine stouter, truncate, and less advanced than rostrum. Orbital border with three small teeth exclusive of post-orbital spine; suborbital margin with one acute spine outside antennal segment and lateral to this a larger truncate spine. Antennal segment with an outer small acute spine and an inner spine more advanced than rostrum bearing a small secondary lateral spine near end. Lateral margin with six spines, first two double, last and smallest one on posterolateral margin. Other spines present on suborbital, subhepatic, subbranchial, pterygostomian regions, and at angle of buccal cavity.

Chelipeds of adult male massive, longer than walking legs; merus armed with eight or nine stout spines on outer margin, others irregularly placed; carpus armed with unequal spines, about five on inner margin; hand deep, compressed, armed above with a more or less double row of spines and on inner surface with two to four spines proximally; fingers curved leaving wide gape, strong tooth near middle of dactyl, tips spooned with edges crenate preceded by a few low tubercles. Adult female with chelipeds no longer and not much stouter than first pair of walking legs; hand tapering somewhat distally;

fingers narrowly gaping with numerous denticles on cutting edges. Walking legs of both sexes spinose and coarsely hairy; propodi elongate and compressed.

Abdomen of male with seven free segments, female with six.

Measurements.—This is the largest species of *Mithrax*. Carapace: male, length, 170 mm., width, 184 mm.; female, length, 77 mm., width, 80 mm.

Variations.—In old males, spines on the chelipeds tend to become blunt and tuberculiform. In medium-sized individuals, the carapace is relatively longer than in the old, spines are sharper, rostral horns curve inward at the sharp tips, the carapace is covered with short hair, chelipeds of both sexes are small, and the gape extends only half the length of the fingers. In young individuals, the spines are even more accentuated, rostral horns are one-fifth as long as the carapace, there are two spines on the suborbital margin outside the antennal segment, chelipeds are no longer or stouter than the first walking legs, and gape of the fingers is less than in older individuals.

Color.—Bright carmine; vinous red with yellowish tints; or thorax dark red; walking legs brick red and chelipeds rose red with yellow fingers (various authors including Rathbun, 1925).

Habitat.—The species is often found among rocks. The carapace is often covered with encrusting organisms; shallow water to 98 fathoms.

Type locality.—Ile-de-France. Locality erroneous.

Known range.—Either North Carolina or South Carolina (?) through Florida Keys and West Indies to Guadeloupe.

Remarks.—Ovigerous females have been reported in May and June from Cuba (Rathbun, 1925).

Mithrax (*Mithrax*) *verrucosus* H. Milne Edwards

Figures 235, 245B

Mithrax verrucosus H. Milne Edwards, 1832, cl. 7, pl. 4 (col.) [+ unpaginated description].—Rathbun, 1925, p. 400, pl. 144 (rev.).

Recognition characters.—Mature males, large-to medium-sized. Carapace covered with flattened, closely crowded granules, nearly naked, granules covered with small pits, cervical suture deep; branchial region with a few dorsal spines on outer part, front and orbit with truncate spines. Rostral



FIGURE 235.—*Mithrax (Mithrax) verrucosus* H. Milne Edwards. Male in dorsal view, legs of left side not shown, 20 mm. indicated.

horns short, separated by a deep notch. Preorbital spine directed somewhat outward, four other spines on orbital margin aside from three occurring on broad basal antennal article. Anterolateral margin with eight spines, first six in pairs, anterior spines of each pair smaller, spines in first two pairs more or less united at base; a single posterolateral spine, and below lateral margin a row of about nine spines.

Chelipeds stout; outer margin of merus with six sharp spines, approximately six spines on upper surface; inner margin of whole cheliped armed with blunt spines or lobes, one on ischium, four on merus, two or three on carpus; carpus with dorsal surface smooth or slightly tuberculate proximally; palm unarmed, elongate, somewhat swollen, fingers gaping with a large tooth near middle of dactyl, edges of spoon-shaped tips slightly crenulate, two bunches of hair inside spoon. Walking legs covered with coarse hair, meri and carpi spiny.

Measurements.—Carapace: male, length, 51 mm.; width, 65 mm.

Variations.—Females, young, and most immature males differ from mature males in that the carapace is covered densely with hair. Rostral horns of females and immature males are shorter and farther apart, but horns of the young are sharper. Spines on the inner margin of the cheli-

peds are sharper, the carpus is more or less spiny dorsally, and the palm is spinulose and hairy above proximally. The degree of spination on the chelipeds also varies individually.

Color.—Dark red; color largely concealed by hairiness, carapace dark dull red, pincers olive above and lighter olive below, tips claret, teeth white, underparts maroon flecked with white and yellow (various authors and Rathbun, 1925).

Habitat.—This species lives near shore among rocks, where it hides in holes. It is nocturnal, and has been caught with the aid of a light while feeding. Shallow water near shore.

Type locality.—Robert Bay, Martinique.

Known range.—Charleston, S.C., through West Indies to Fernando Noronha Island (225 miles northeast Cape São Roque), Brazil.

Remarks.—Pearse (1932a) determined freezing point of blood in this species at Tortugas (range -1.99° to -2.24° C.).

***Mithrax (Mithrax) hispidus* (Herbst). Coral crab**

Figures 236, 245C

Cancer hispidus Herbst, 1790, p. 245 (247 by error), pl. 18, fig. 100.

Mithrax hispidus: Rathbun, 1925, p. 406, text-fig. 124, pls. 145–146; pl. 147, fig. 3 (rev.).

Recognition characters.—Carapace swollen, considerably wider than long, smooth except for some low, rounded prominences chiefly toward outer margin of branchial region, gastric tubercles



FIGURE 236.—*Mithrax (Mithrax) hispidus* (Herbst). Male in dorsal view, legs of left side not shown, 20 mm. indicated.

faint; front wide. Rostral horns short, obtuse, separated by a U-shaped notch. Preorbital angle blunt, slightly produced. Basal article of antenna with two teeth, inner one nearly as advanced as rostrum, outer smaller one on orbital border. Orbit with four tubercles on margin, two superior much smaller than external or inferior ones. Anterolateral margin with four spiniform teeth, first one obtuse, often bifid at tip; second longer, sharp, double, and curving forward; third and fourth slender. Posterolateral border with a smaller tooth situated higher on carapace in line with two obliquely located tubercles, or a low spine and a tubercle. Subhepatic region with two tubercles; a few other tubercles on subbranchial and pterygostomian regions.

Chelipeds large, unequal in males, equal in females; merus with four or five spines and a few tubercles on upper surface and two spines on inner margin; carpus smooth; hand smooth; fingers spooned at tips, gaping, with a broad low crenulated tooth near base of dactyl.

Measurements.—Carapace: large male, length, 102 mm.; width, 146 mm.

Variations.—Young individuals have tubercles on the carapace more protuberant than in the old.

Color.—Nearly uniform deep brownish-red or terra cotta color above, brighter on chelipeds and darker on legs (due to brown hairs); legs often with brighter red bands at joints; underparts of body mostly white or bluish white; legs red, speckled with pale yellow (Verrill, 1908).

Habitat.—Commonly lives on rough bottom; shallow water to 30 fathoms.

Type locality.—Unknown.

Known range.—Recorded in literature from as far north as Delaware Bay (Say, 1818), off Charleston Harbor, S.C., and Georgia (Gibbes, 1850). Bahamas and Florida Keys through West Indies to São Paulo, Brazil; Bermuda.

Mithrax (Mithrax) pleuracanthus Stimpson

Figures 237, 245D

Mithrax pleuracanthus Stimpson, 1871a, p. 116.—Milne Edwards, 1875, p. 95, pl. 20, figs. 3–3f.—Rathbun, 1901, p. 68.—Hay and Shore, 1918, p. 458, pl. 38, fig. 3.—Rathbun, 1925, p. 411, pl. 150 (rev.).

Mithrax depressus Milne Edwards, 1875 (in part), p. 96, pl. 20, figs. 4–4c.—Rathbun, 1901, p. 68.—Verrill, 1908, p. 407, pl. 23, fig. 1.—Hay and Shore, 1918, p. 458, pl. 38, fig. 2.

Mithrax hispidus Rathbun, 1892 (in part), p. 265.

Recognition characters.—Carapace not much wider than long, conspicuously tuberculate; front



FIGURE 237.—*Mithrax (Mithrax) pleuracanthus* Stimpson. Animal in dorsal view, legs of left side not shown, 10 mm. indicated.

wide. Rostral horns shorter and wider than in *M. hispidus*, notch between horns narrower and nearly triangular, always triangular in young individuals. Preorbital angle blunt, slightly produced; orbit with two superior tubercles; a small postorbital angle and a suborbital tubercle. Basal article of antenna with two teeth, inner one nearly as advanced as rostrum, outer smaller one on orbital border. Spines of anterolateral border well developed, anterior one or two inclined to be double, posterior two more acute and pointed forward, small tubercles about base of spines. Gastric region with transverse row of five tubercles, in front of these, two pairs of tubercles, anterior pair at base of rostral horns. Mesogastric region with two tubercles on each side in a transverse line. Cardiac region with three poorly defined tubercles. Branchial area with four rather strong tubercles and several smaller ones arranged more or less in three oblique rows radiating from cardiac region to anterolateral border.

Chelipeds large; merus with scattered low spines on upper margin, with a simple spine, spine and tubercle, or rounded eminence on inner margin, and five small spines on posterior border; carpus smooth or with a few low tubercles on upper surface; hands smooth; fingers slightly gaping, dentate for nearly entire length, spoon-shaped at tips. Walking legs dentate and hairy.

Measurements.—Carapace: large male, length, 36 mm., width, 43 mm.; ovigerous female, length, 16 mm., width, 19 mm.

Variations.—In young individuals the rostral horns are wider behind and flatter than in adults; the notch between the rostral horns in extremely large individuals may be U-shaped; the large tubercle above the posterolateral margin may be spiniform but is located higher on the carapace than the similarly formed tubercle in *M. hispidus*.

Color.—Carapace yellowish white, with blotches of bright red; two largest red spots over branchial areas, a median spot on cardiac area, a pair situated farther back, a small pair behind orbits, and another beneath orbits; legs yellowish white, blotched or barred with red; chelae light red with pale tips (Verrill, 1908, for *M. depressus*).

Habitat.—This species, which is often encrusted with bryozoans and other organisms, is found predominantly on coarse or rocky substrates but occasionally on muddy or sandy bottom. In North Carolina it is a common species on the offshore banks and is associated with *Mithrax forceps*. Pearse (1934) found the species in canals of the sponge *Stematumenia strobilinia* (Lamarck) at Tortugas, Fla. Shallow water to 28 fathoms.

Type localities.—Key West, 2–5 fathoms, Tortugas, 5–6 fathoms [Fla.]; St. Thomas.

Known range.—Beaufort, N.C., to Pensacola, Fla.; Yucatan Channel off Cape Catoche, Mexico, and Gulf of Campeche; West Indies to Venezuela; Bermuda.

Remarks.—Ovigerous females are known in Florida from December to February, and in August. They are known from North Carolina in April, St. Thomas in July, and Venezuela in September (Rathbun, 1925; U.S. National Museum records).

***Mithrax (Mithraculus) forceps* (Milne Edwards)**

Figures 238, 245E

Mithraculus forceps Milne Edwards, 1875, p. 109, pl. 23, fig. 1.
Mithrax forceps: Hay and Shore, 1918, p. 457, pl. 38, fig. 1.—
Rathbun, 1925, p. 431, pl. 156 (rev.).

Recognition characters.—Carapace about one-fifth wider than long, deeply sculptured in young individuals but smoother with age. Anterolateral margin with four tubercles or teeth exclusive of postorbital angle, separated by broad rounded sinuses, first tooth usually shortest, remainder usually acute and turned forward at tip. Three

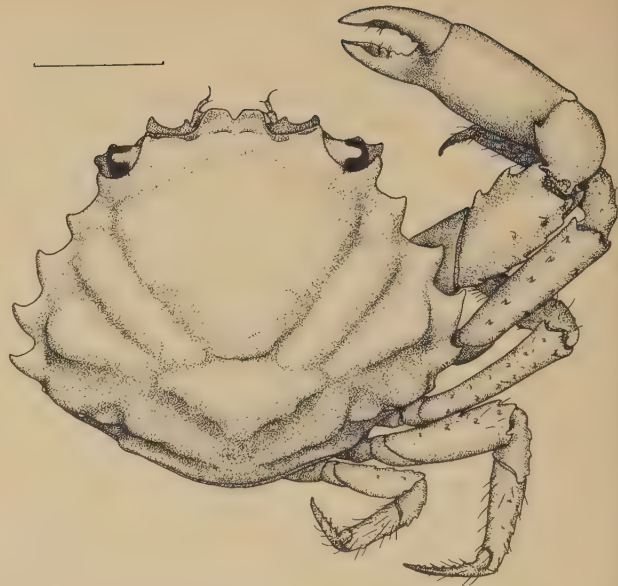


FIGURE 238.—*Mithrax (Mithraculus) forceps* (Milne Edwards). Male in dorsal view, legs of left side not shown, 5 mm. indicated.

grooves running diagonally backward over branchial area from near first, second, and fourth sinuses of anterolateral margin, between these grooves two well-defined, unbroken ridges and a broken ridge behind third groove. Cardiac and gastric regions crossed by less sharply defined ridges somewhat broken up into low rounded tubercles. Notch between rounded rostral horns broadly V-shaped, two pairs of tubercles on frontal region behind lobes of rostrum. Preorbital angle prominent, not exceeding rostrum. Orbital margin with a dorsal and ventral tubercle near postorbital angle. Outer spine of fused antennal article nearly equaling rostrum.

Chelipeds strong. Merus with two strong spines or tubercles in front, five much smaller ones on posterior margin, and usually two on upper surface near posterior margin. Carpus smooth or with a small spine or tubercle on inner margin near inner distal angle. Hand smooth, polished, somewhat tumid. Fingers widely gaping in male, with expanded hollowed-out tips; dactyl with single large tooth one-third distance from proximal end, or with a few minute teeth; immovable finger with from one to three small teeth or tubercles in middle. Walking legs spiny or denticulate with many fine hairs.

Measurements.—Carapace: male, length, 21 mm.; width, 25 mm.

Color.—Red, approaching vermilion, with occasional trace of purple. Terra cotta, or uniform yellowish brown, varying to greenish brown; often with a wide, pale yellow, median dorsal stripe, and legs often banded, especially in young individuals (various authors).

Habitat.—The species lives on rocky shores and reefs in crevices, under stones and dead coral; also exposed between tides and in shallow water in certain areas (Verrill, 1908). In North Carolina this form is found on offshore reefs and has been found in the sponge *Stematumenia strobilinia* (Lamarck) at Dry Tortugas, Fla. (Pearse, 1934). Intertidal to 30 fathoms.

Type locality.—Guiana.

Known range.—From Cape Hatteras, N.C., through Gulf of Mexico to Rio de Janeiro, Brazil; Bermuda.

Remarks.—Ovigerous females have been taken in Florida from November to February and from June to August; they are known from the Gulf of Mexico in February, Curaçao in April, Barbados and Aruba in midsummer, and from Venezuela in September and November (Rathbun, 1925; U.S. National Museum records). Some of the larval stages have been described by Lebour (1944).

Genus *Microphrys* H. Milne Edwards, 1851

Garth, 1958, p. 385.

KEY TO SPECIES IN THE CAROLINAS

- a. Carapace without lateral laminiform processes; one strong branchial spine.....*bicornutus* (p. 259).
- aa. Carapace with two lateral laminiform processes; two strong branchial spines.....*antillensis* (p. 260).

Microphrys bicornutus (Latreille)

Figures 239, 245F

Pisa bicornuta Latreille, 1825, p. 141.

Microphrys bicornutus: Hay and Shore, 1918, p. 459, pl. 38, fig. 10.—Rathbun, 1925, p. 489, text-fig. 139, pl. 175 (rev.).

Recognition characters.—Carapace subtriangular, moderately hairy, all raised parts covered with rounded tubercles; a line of four tubercles arching upward on intestinal region, branchial region with two or three short spines and another spine at lateral angle. Rostrum composed of two stout horns, divergent throughout or divergent at base with extremities curving inward, one-half to one-third length of remainder of carapace. Basal



FIGURE 239.—*Microphrys bicornutus* (Latreille). Male in dorsal view, legs of left side not shown, 10 mm. indicated.

article of antenna with a conspicuous, flat, obtuse spine at anterior angle and behind this a marginal tubercle or a short stout spine in old individuals. Orbits small, circular, with closed fissures, eyes small, preorbital angle rectangular.

Chelipeds spotted, spots persisting for many years in alcohol; merus with three or four tubercles or short, blunt spines above; carpus somewhat nodose; hand smooth; fingers gaping, hollowed out at tips. Walking legs diminishing noticeably in length from first to fourth pair, hairy, margins somewhat rough.

Abdomen of both sexes with seven separate segments.

Measurements.—Carapace: male, length, 36 mm., width, 26 mm.; female, length, 24 mm., width, 20 mm.

Color.—Variable; carapace often dull yellowish brown or bright purplish rose; chelipeds grayish white, covered with small, round, purplish spots.

Habitat.—The species is common on coral reefs. It is often disguised by foreign objects such as sponges, anemones, hydroids, algae, etc., which

became attached to it. Shallow water to 16.5 fathoms.

Type locality.—*Nouvelle Hollande*.

Known range.—Near Beaufort, N.C., to Cedar Keys, Fla.; Bahamas to Florianopolis, Santa Catarina, Brazil; Bermuda.

Remarks.—Ovigerous females have been reported from March to August in the Caribbean area, and from November to January in the West Indies, Venezuela, and Brazil (Rathbun, 1925; U.S. National Museum records).

Pearse (1932b), working at Dry Tortugas, listed the copepod *Anthiacus intermedius* from the gill lamellae (accidental guest) and a tape-worm plerocercoid, *Rhynchobothrus*, from the viscera, and (in Wilson, 1935) reported a few specimens of *Cancericola jamaicensis* Wilson from the branchial cavity of this crab.

***Microphrys antillensis* Rathbun**

Figures 240, 245G

Microphrys antillensis Rathbun, 1920, p. 20.—1925, p. 498, text-fig. 141, pl. 176, figs. 3–4 (rev.).

Microphrys platysoma: Hay and Shore, 1918, p. 459, pl. 38, fig. 9.

Recognition characters.—Carapace depressed, tuberculate, and granulate, area at inner angle of branchial region finely granulate; intestinal region with four large, equal tubercles. Anterolateral wall with two laminiform processes, one on hepatic, one on branchial region; hepatic process with anterior end acute, projecting outward and occasionally forward in large individuals, sometimes with outward-projecting tubercle at middle of upper edge; a spine between and below level of hepatic and branchial processes; branchial process not rimmed nor sharply defined. Branchial region with three spines, one forming posterolateral angle occasionally doubled. Posterior margin with row of tubercles increasing in size medially. Rostral horns slender, directed forward, about one-sixth length of remainder of carapace. Basal article of antenna with spine at outer angle about half length of rostral spines. Orbits small, circular, with closed fissures; eyes small; preocular spines acute, about half as long as antennal spines.

Merus of chelipeds with dentate and laminate dorsal crest; carpus tuberculate; palm less than twice as long as broad; fingers widely gaping, immovable finger strongly curved downward. Walking legs sparsely hairy and with a few spines and



FIGURE 240.—*Microphrys antillensis* Rathbun. Male in dorsal view, legs of left side not shown, 5 mm. indicated.

tubercles; propodi with prominent distal laminiform process for articulation of dactyls.

Abdomen of both sexes with seven free segments.

Measurements.—Carapace: male, length, 18 mm.; width, 16 mm. Length of rostral horns, 3 mm.

Habitat.—Two to 15 fathoms.

Type locality.—Off Montego Bay Point, Jamaica.

Known range.—Beaufort Harbor, N.C., to Cape Fear, N.C.; Cuba; Jamaica; Puerto Rico.

Remarks.—Ovigerous females have been reported in September from North Carolina (Rathbun, 1925), in June from Florida, and November from Bimini (U.S. National Museum records).

Genus *Stenocionops* Desmarest, 1823

Garth, 1958, p. 401.

KEY TO SPECIES IN THE CAROLINAS

- a. Hepatic region not enlarged nor produced beyond general outline of carapace, armed with not more than one large spine.

b. Marginal spines behind orbit four, carapace with about four median spiniform tubercles

furcata coelata (p. 261).

bb. Marginal spines behind orbit three, carapace with about eight median spines

spinimana (young) (p. 262).

aa. Hepatic region enlarged and produced separately from curve of branchial region, marginal hepatic spines 3; carapace with 12 or 13 median spines

spinimana (adult) (p. 262).

Stenocionops furcata coelata (Milne Edwards)

Figures 241, 245H

Pericera coelata Milne Edwards, 1878, p. 224.

Stenocionops furcata coelata: Hay and Shore, 1918, p. 460, pl. 39, fig. 3.—Rathbun, 1925, p. 540, pl. 164 (rev.).

Recognition characters.—Carapace oblong-ovate, approximately three-fourths as wide as long, uneven, with strong spines and a dense covering of short setae and many scattered, longer, hooked hairs. Rostrum consisting of two nearly straight diverging horns with rows of hooked setae. Orbital region broad, eyes small, retractile within tubular orbits; preorbital spine strong, suborbital and postorbital spines much smaller.



FIGURE 241.—*Stenocionops furcata coelata* (Milne Edwards). Male in dorsal view, legs of right side in part after Rathbun (1925), legs of left side not shown, 20 mm. indicated.

Basal antennal article enlarged, armed with one or two small distal spines or tubercles not visible dorsally. Middorsal line with four strong spiniform tubercles, one on gastric region, remainder on cardiac and intestinal regions, fourth spine with tip curved forward. Lateral border with four stout spines, one on hepatic, remainder on branchial region; in addition, two other stout spines on branchial region and various smaller ones toward front. Ventral surface of body, except distal articles of chelipeds, closely covered with bulbous setae hiding carapace.

Chelipeds in adult males fairly large and nodose; hand long, cylindrical, and granulate; fingers approximately half as long as palm, gaping in basal half, a tooth on dactyl near base. In other individuals chelae weak; fingers less than half as long as palm; merus with strong spines above near distal end preceded by several smaller spines. Walking legs moderately elongate, more or less rough with clusters of hooked hairs, articles subcylindrical.

Abdomen in male and female with seven distinct segments.

Measurements.—Carapace: large male, length, 137 mm.; width, 111 mm. Length rostral horn, 26 mm. Carapace: smaller male, length, 91 mm.; width, 64 mm. Length rostral horn, 25 mm.

Variations.—Large specimens have relatively shorter rostral horns than smaller individuals; young specimens are smoother than old ones.

Color.—Dark red.

Habitat.—This species is found on a variety of bottoms, including fine white sand, yellow sand, coarse gray sand, sand with algae, sandy shell, broken shell, and coral. It has been reported most often from coarse bottom (Rathbun, 1925), and occurs on shelly reefs off Beaufort Inlet, N.C. Shallow water near shore to 60 fathoms, rarely to 278 fathoms.

Type localities.—Ten miles from Jolbos Islands [Yucatan], and near Havana [Cuba], 175 fathoms.

Known range.—Off Beaufort, N.C., to northwest Florida and Alabama; Yucatan Channel; West Indies to Barbados.

Remarks.—This species is similar to the typical subspecies *S. f. furcata* which ranges from Georgia to Bahia, Brazil, in shallow water near shore to 35 fathoms depth. The typical subspecies has the carapace more evenly sculptured and is

less spinous than *S. f. coelata* (Rathbun, 1925, p. 449).

Ovigerous females are known in Florida from March to August (U.S. National Museum records).

***Stenocionops spinimana* (Rathbun)**

Figures 242, 245I

Libinia spinimana Rathbun, 1892, p. 240, pl. 30.

Stenocionops spinosissima: Hay and Shore, 1918, p. 460, pl. 39, fig. 2.

Stenocionops spinimana: Rathbun, 1925, p. 457, pl. 267 (rev.).

Recognition characters.—Carapace subpyriform, convex, covered with sparse growth of short, fine, curled hairs; 8 to 13 median dorsal spines, and numerous other spines on gastric and branchial regions; anterior marginal hepatic spines 3, anterior-most spine small and occasionally absent in old individuals. Rostral horns widely divergent, straight, tapering gradually to slender tip. Orbits tubular, not strongly projecting, eyes small, retractile within orbits; preorbital spine acute, curving forward slightly at tip; postorbital spine similar in size to spine near anterolateral angle of basal article of antenna.

Merus and carpus of chelipeds with numerous spines, hand rough throughout length with two rows of spines above, one below, spines becoming progressively smaller distally. Walking legs with a few spines. Meral articles with a terminal spine above, and on first leg a longitudinal inner-upper row of five or six, and a ring of about four spines near distal end; on second leg a ring of three or four; on third and fourth only one or two spines besides terminal one. Carpus of first leg with three or four spines, second with three spinules or tubercles, third and fourth with one.

Abdomen in male and female with seven segments, six free in females.

Measurements in millimeters	Large male	Holotype of <i>spinimana</i> (male)	Half-grown male	Young female
Length of carapace, including horns....	130	89	53	18
Width of carapace, including spines....	118	76	42	13
Width of carapace, excluding spines....	110	69	36	10
Length of rostral horns.....	11	10	10	3

Variations.—This species exhibits great change in shape and spination with increasing age, as has



FIGURE 242.—*Stenocionops spinimana* (Rathbun). Holotypic male in dorsal view (after Rathbun, 1892).

been pointed out by Rathbun (1925), and Garth (1958) for related forms. Young individuals are much different in shape from adults, having a width considerably less than length (width about 70 percent of length including spines and rostrum), whereas the mature animals are more rounded in contour (large adult male, with about 90 percent of length). Old individuals have a thicker coating of hair than immature ones, especially on the chelipeds. Chelipeds in old individuals become quite large and stout with the palm compressed (length more than twice that of carapace). The young have fewer spines than adults, the hepatic region is not expanded and bears only one marginal spine as opposed to three spines in adults.

Habitat.—The species has been found on a variety of bottoms, from gray mud, through various grades of sand, to sand-shell, coral, and rock (Rathbun, 1925). Twenty to 124 fathoms.

Type locality.—Off Cape Lookout, N.C., 124 fathoms.

Known range.—Off Cape Hatteras, N.C., to Florida Straits and Gulf of Mexico off Mobile Bay, Ala.

Remarks.—Ovigerous females have been reported from South Carolina in December (Rathbun, 1925).

Genus *Macrocoeloma* Miers, 1879

Garth, 1958, p. 412.

KEY TO SPECIES IN THE CAROLINAS

- a. Carapace without dorsal spines in addition to epibranchial and posterior spines—*trispinosum* (p. 263).
- aa. Carapace with dorsal spines in addition to epibranchial and posterior spines—*camptocerum* (p. 264).

Macrocoeloma trispinosum (Latreille). Grass crab, sponge crab, decorator crab

Figures 243, 245J

Pisa trispinosa Latreille, 1825, p. 142.

Macrocoeloma trispinosum: Hay and Shore, 1918, p. 457, pl. 38, fig. 11.—Rathbun, 1925, p. 466, text-fig. 132, pl. 166, fig. 1; pl. 167 (rev.).

Recognition characters.—Carapace irregularly triangular, body and legs with velvety covering of short brown hairs, thick and swollen, wide at level of orbits, narrowing distinctly in hepatic portion, widening again posteriorly. Middorsal region much elevated and bearing four low, rounded tubercles or bosses, one on gastric, one on cardiac, and one on each epibranchial region.

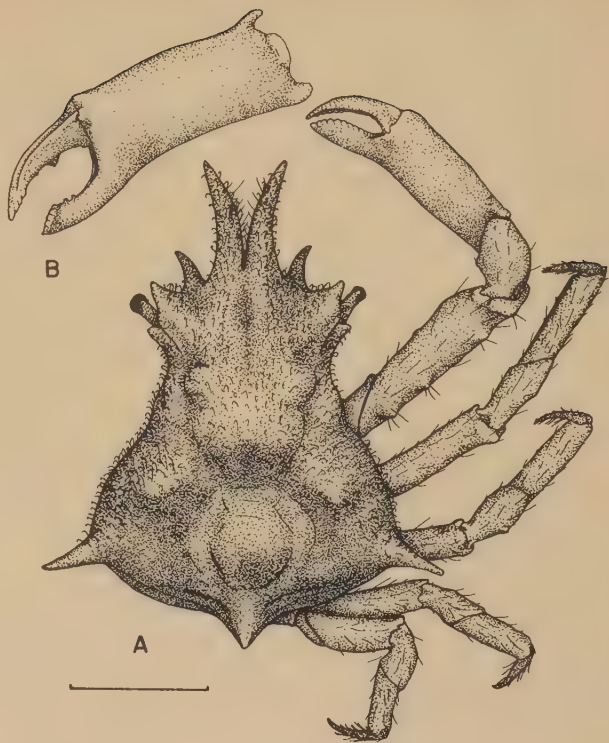


FIGURE 243.—*Macrocoeloma trispinosum* (Latreille). A, small male in dorsal view, legs of left side not shown, 10 mm. indicated; B, right chela of adult male in frontal view.

Posterolateral angle prolonged into a long flattened spine directed obliquely outward and backward, sometimes curved upward; posterior margin with broad, median, triangular projection with tip sometimes slightly recurved. Rostrum formed of two somewhat flattened horns adjacent and subparallel at base, divergent distally. Eyes retractile within roomy, projecting, tubular orbits, upper margin of orbit deeply emarginate, pre- and post-ocular teeth prominent, preocular teeth curved forward. Basal article of antenna with inner angle produced, exceeding frontal margin, and forming a broad spine directed obliquely outward at each side of rostrum.

Chelipeds of male narrow, approximately as long as carapace; merus nodose; palm with subparallel sides; dactyl approximately half as long as upper margin of palm and lightly furrowed above. Walking legs rather slender, slightly nodose.

Abdomen with seven separate segments in both sexes.

Measurements.—Carapace: male, length, 34 mm.; width, 29 mm.

Variations.—Rathbun (1925) discussed variation in this species throughout its known range. Body shapes falling into three general series are distinguishable. In the first, the typical form, the posterolateral prominences are narrow, with regularly tapering spines, projecting beyond the general outline of the carapace and directed more or less backward, and sometimes strongly curved from base to tip with the concavity forward. The carapace is considerably constricted behind the orbits. The orbits are prominent owing to this constriction, and the pre- and post-ocular teeth are strong, the former directed forward and curved. The upper edge of the orbit is deeply emarginate. The four large tubercles or bosses are prominent, some or all with an acute tip, that on the gastric region sometimes nearly a spine.

In the second series, treated by Rathbun as an unnamed variety, the posterolateral prominences are wider than in the first series, less spinelike and more laminate, their hind margins nearly transverse. The carapace is less narrowed behind the orbits, the orbital teeth less marked, though the preocular tooth is directed forward and a little curved, and the superior emargination less deep. The four large dorsal bosses are lower than in series one, but the gastric boss tends to be surmounted by a sharp tubercle or granule.

In series three, called *M. t. nodipes*, the posterolateral prominences are broader and more obtuse than in series two with their margins almost continuing the margin of the carapace. The carapace is constricted little or not at all behind the orbits; the preocular tooth is acute but not prominent, and the postocular tooth blunt or subacute with both teeth somewhat more prominent in young individuals than in old ones. The orbit has a slight emargination in the upper border. The dorsal bosses are lower than in the other series, smoothly rounded and blunt.

In the three series the posterior median spine varies in a manner similar to the lateral spines. Within the three series, the rostrum shows great variability in length, direction, and curvature of the horns.

Color.—Hairs yellowish or reddish brown (various authors).

Habitat.—In North Carolina, this species has been found in seaweed in Beaufort Harbor, in the ocean on floating masses of *Sargassum*, and dredged from offshore reefs. Elsewhere it has been found in a variety of situations, from pilings and mangrove roots to weedy rocks, coarse-coral sand, sand-shell, and broken-shell bottoms. The species is often concealed by a covering of sponge. Shallow water to 45 fathoms.

Type locality.—Nouvelle Holland (?) [error].

Known range.—Beaufort, N.C., to Alligator Harbor, Fla.; Yucatan; through West Indies to off Cape São Roque, Brazil.

Remarks.—Ovigerous females have been reported from southern Florida in December, Cuba in April, and Jamaica and St. Thomas in July (Rathbun, 1925; U.S. National Museum records).

Macrocoeloma camptocerum (Stimpson)

Figures 244, 245K

Pericera camptocera Stimpson, 1871a, p. 112.

Macrocoeloma camptocercum: Hay and Shore, 1918, p. 457, pl. 38, fig. 12.—Rathbun, 1925, p. 469, pl. 174, fig. 4; pl. 270, fig. 2 (rev.).

Recognition characters.—Carapace irregularly triangular; surface covered with short, close



FIGURE 244.—*Macrocoeloma camptocerum* (Stimpson). Male in dorsal view, legs of left side not shown, 10 mm. indicated.

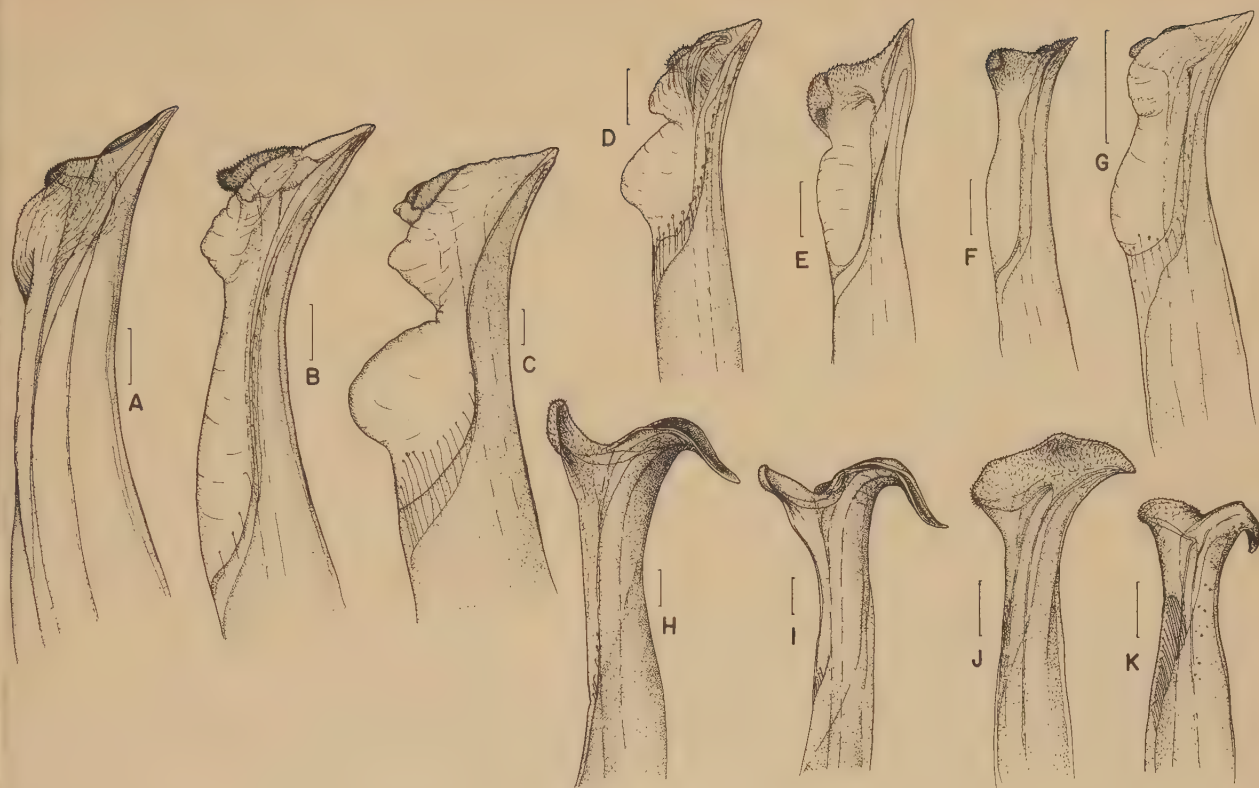


FIGURE 245.—Subfamily Mithracinae, tips of right first pleopods of males; A, *Mithrax spinosissimus* (Lamarck), sternal view; B, *Mithrax verrucosus* H. Milne Edwards, sternal view; C, *Mithrax hispidus* (Herbst), sternal view; D, *Mithrax pleuracanthus* Stimpson, sternal view; E, *Mithrax forceps* (Milne Edwards), sternal view; F, *Microphrys bicornutus* (Latreille), sternal view; G, *Microphrys antillensis* Rathbun, sternal view; H, *Stenocionops furcata coelata* (Milne Edwards), sternal view; I, *Stenocionops spinimana* (Rathbun), sternal view; J, *Macrocoeloma trispinosum* (Latreille), lateral view; K, *Macrocoeloma camptocerum* (Stimpson), lateral view; 0.33 mm. indicated.

pubescence, and, in addition, long, stiff, curled hairs on front, gastric region, and lateral portions of branchial regions; wide at level of orbits, narrowing distinctly in hepatic portion, widening again posteriorly; with four strong spines on dorsal region, one on gastric, one on cardiac, and one on each epibranchial region. Posterolateral spines subconical, regularly tapering, acute, and directed slightly backward; posterior median spine shorter, acute, obliquely erect. Rostral horns acute, rather regularly divergent from base. Spines on basal article of antennae rather slender, divergent. Orbital tubes, pre- and post-orbital spines protuberant laterally, preorbital spine curving a little forward.

Chelipeds of male strong, longer than carapace; merus with a few short spinules above; carpus

somewhat nodose with a tubercle at inner angle; palm widest near articulation; fingers tipped with black or dark brown. Walking legs nearly smooth.

Abdomen with seven separate segments in both sexes.

Measurements.—Carapace: male, length, 40 mm., width, 36 mm.; female, length, 24 mm., width, 20 mm.

Variations.—The rostral horns may be straight or slightly curved outward at tips, and range in length from one-sixth to one-third the total length of the carapace. The interspace between horns may vary from a narrow V-shape to almost a right angle. The posterolateral spine may be straight in frontal section or curved upward and nearly transverse or directed strongly backward.

Color.—A dirty brown.

Habitat.—The species has been taken on a variety of bottoms ranging from sand with grass, or a hard smooth substrate, to rocky or coral bottoms. Rathbun (1925) reported the form from predominantly coarse bottoms. About 2 to 13 fathoms.

Type locality.—Near Key West [Fla.], in from 2 to 5 fathoms.

Known range.—Beaufort Harbor, N.C., via southern Florida to Alligator Harbor, Fla.

Remarks.—Ovigerous females are known in Florida from January to March (U.S. National Museum records).

Family Parthenopidae

Eyes usually retractile within small, circular, well-defined orbits, floor of orbit nearly continued to front, leaving a hiatus usually filled by second [article] of antennary peduncle. Basal antennal [article] small, deeply imbedded between inner angle of orbit and antennular fossae. Antennules folding somewhat obliquely (Alcock, 1895).

Subfamily Parthenopinae

Carapace commonly equilaterally triangular, sometimes subpentagonal or ovate-pentagonal, and sometimes almost semicircular or semielliptical in outline. Cardiac and gastric regions usually deeply marked off from branchial regions on either side, making dorsal surface of carapace trilobed. Rostrum simple or obscurely trilobed. Chelipeds vastly longer and more massive than walking legs (Alcock, 1895). First pleopod varying, more or less stout, apically tapering or not tapering; second pleopod usually short and of usual shape (Stephensen, 1945).

KEY TO GENERA IN THE CAROLINAS

(Modified after Rathbun, 1925)

- a. Carapace not laterally expanded over walking legs.
- b. Carapace tuberculate or eroded—*Parthenope* (p. 266).
- bb. Carapace smooth, except for a few strong spines
Solenolambrus (p. 270).
- aa. Carapace more or less expanded forming a vault beneath which walking legs are concealed
Heterocrypta (p. 270).

Genus *Parthenope* Weber, 1795

Garth, 1958, p. 434.

KEY TO SPECIES IN THE CAROLINAS

- a. Carapace ovate-pentagonal, surface scarcely carinate in adult (Subgenus *Parthenope*)-----*agona* (p. 266).
- aa. Carapace broadly triangular, carinate or tuberculate, with more or less rounded sides
(Subgenus *Platylambrus*).
- b. Carapace and chelipeds very flat; spine at end of main dorsal branchial ridge small—*serrata* (p. 267).
- bb. Carapace convex, chelipeds not flat; spine at end of main dorsal branchial ridge large.
- c. Carapace much broader than long; hand with 8-12 teeth on inner, 10-12 on outer margin
pourtalesii (p. 268).
- cc. Carapace not much, if any, broader than long; hand with few good sized marginal teeth, six to eight on inner, three to five on outer margin
fraterculus (p. 269).

Parthenope (Parthenope) agon (Stimpson)

Figures 246, 252A

Lambrus agonus Stimpson, 1871a, p. 131.

Parthenope agon: Hay and Shore, 1918, p. 462, pl. 39, fig. 5.

Parthenope agonus: Rathbun, 1925, p. 513, text-fig. 146, pls. 178-179; pl. 275, figs. 1-3 (rev.).

Recognition characters.—Carapace ovate-pentagonal or subcircular, somewhat broader than long, with rounded sides, without angles. Post-orbital constriction slight, not involving pterygostomian ridge continuing from lower side of orbit to point above cheliped. Depressions be-

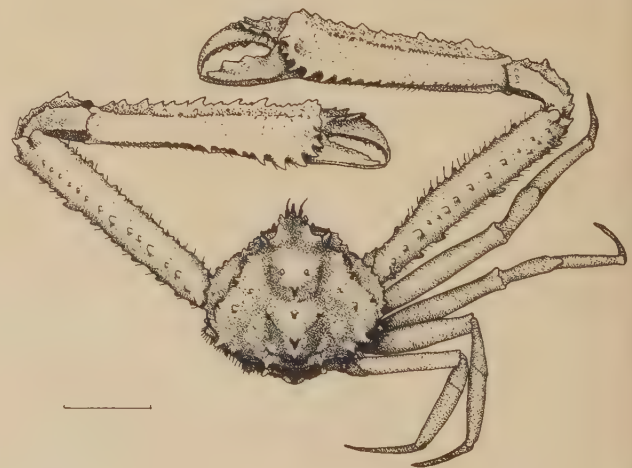


FIGURE 246.—*Parthenope (Parthenope) agon* (Stimpson). Male in dorsal view, position of legs reconstructed, walking legs of left side not shown, 10 mm. indicated.

tween regions of carapace not markedly deep; surface coarsely punctate or eroded, and with numerous granules and tubercles, larger tubercles more or less spiniform and arranged as follows: five on gastric region, three on cardiac, one on each side of urocardiac lobe, five on branchial, and one on each hepatic region. Anterolateral margin of branchial region with six small teeth, below and behind last tooth a broad triangular tooth, and still lower on ventral surface a spine visible between ischia of cheliped and first leg. Median rostral tooth narrow, produced, denticulate at base, an acute forward-pointing tooth over each antennular cavity. Orbit with several spines on outer margin, a suture above, open below; eye with small spine on upper surface. A conical spine or tubercle on each side of sternum near base of chelipeds.

Chelipeds long, slender (length of merus approximately 1.3 times width of carapace), prismatic, upper surface finely rugose. Merus and carpus with an irregular row of dentiform tubercles near middle of upper surface, on inner and outer margins, and near outer margin of hand. Upper margin of hand with row of 18–20 irregular teeth, largest near base of fingers but decreasing in size both proximally and distally; outer margin with 4 to 6 larger teeth and many intermediate smaller ones. Walking legs long, slender, bare, and almost smooth.

Second segment of abdomen with sharp transverse crest.

Measurements.—Carapace: male, length, 20 mm.; width, 21 mm. Length of merus, 30 mm.

Variations.—The rostrum may be broadly triangular, subentire, instead of tridentate with denticulate margins. In young individuals the pterygostomian ridge is less developed anteriorly, and the postorbital constriction is more evident.

Color.—Light buff, somewhat marbled with purple, chelipeds and legs with broad bands of purple.

Habitat.—The species has been reported from predominantly sandy or broken-shell bottom (Rathbun, 1925); 25 to 115 fathoms.

Type localities.—Off the Marquesas, Carysfort Reef, and Conch Reef, 40 and 49 fathoms [southern Florida].

Known range.—Off Capes Hatteras and Lookout, N.C.; Gulf of Mexico near Pensacola, Fla.,

through Florida Straits; Puerto Rico; Trinidad; between British and Dutch Guiana.

Remarks.—Ovigerous females have been taken from southwestern Florida in March (Rathbun, 1925), and off the Guianas in September (U.S. National Museum records).

Parthenope (Platylambrus) serrata (H. Milne Edwards)

Figures 247, 252B

Lambrus serratus H. Milne Edwards, 1834, p. 357.

Platylambrus serratus: Hay and Shore, 1918, p. 463, pl. 39, fig. 7.

Parthenope serrata: Rathbun, 1925, p. 516, pls. 180–181; pl. 275, figs. 7–10 (rev.).

Recognition characters.—Carapace depressed, width approximately 1.5 times length; convex anterolateral margin of branchial region with seven to nine triangular teeth in front of long, flat, lateral spine. Posterolateral margin concave; posterior margin convex, wide, both margins together with seven tubercles noticeably larger than others, each terminating an indefinite longitudinal or oblique line of tubercles. Elevations of carapace ornamented with numerous unequal granulated tubercles; depression between gastric and branchial regions deep. Rostrum short, tridentate, narrow at tip, and with raised margin continuous with superior wall of orbits. Pterygostomian and subhepatic regions with an excavation reaching margin of orbit and, with chelipeds retracted, forming covered efferent passages.

Chelipeds, when extended, approximately 2 to 2.5 times as long as carapace, trigonal, smooth beneath, more or less tuberculate on upper sur-



FIGURE 247.—*Parthenope (Platylambrus) serrata* (H. Milne Edwards). Male in dorsal view, 10 mm. indicated.

face, and with margins cut into lanceolate or triangular teeth fringed with fine hairs, much stronger on outer than on inner side of articles; hand with about nine teeth alternately large and small; fingers stout, oblique. Walking legs of moderate size, longest not exceeding merus of cheliped.

Abdomen of male with segments three to five fused, sixth segment with a median spine.

Measurements.—Carapace: male, length, 19 mm.; width, 28 mm. Length of cheliped, 60 mm.

Color.—Red somewhat mottled with gray; fingers carmine, shading to black.

Habitat.—The species has been reported from a variety of bottoms ranging from coral to fine sand and mud, but it has been taken most often from muddy or sandy bottoms (Rathbun, 1925; Holthuis, 1959). Shallow water to 60 fathoms.

Type locality.—*l'Océan indien* [erroneous locality].

Known range.—Off the three North Carolina capes, Gulf of Mexico from Pensacola to southern Florida, and off Campeche, Mexico; West Indies to Bahia, Brazil.

Remarks.—Hildebrand (1955) and Holthuis (1959) added distributional extensions to Campeche and Surinam. Ovigerous females have been reported in May and June from Surinam (Holthuis, 1959). They are known from North Carolina in June, Florida in summer, and Cuba in October (U.S. National Museum records).

***Parthenope (Platylambrus) pourtalesii* (Stimpson)**

Figures 248, 252C

Lambrus pourtalesii Stimpson, 1871a, p. 129.

Parthenope pourtalesii: Hay and Shore, 1918, p. 462, pl. 39, fig. 6.—Rathbun, 1925, p. 521, pls. 182, 183, and 276 (rev.).

Recognition characters.—Carapace broadly ovate-triangular, convex; branchial regions rather deeply separated from gastric, cardiac, and hepatic regions. Posterolateral angle marked by conspicuous laciniated spine located behind bulging curve of anterolateral margin; hepatic margin armed with a small but prominent spine. Anterolateral margin behind cervical suture armed with eight or nine teeth and spines, first three or four shorter than remainder. Posterolateral margin with three or four unequal spines in addition to large one on ridge; posterior margin with three large and several small spines. General surface of carapace pitted and eroded,



FIGURE 248.—*Parthenope (Platylambrus) pourtalesii* (Stimpson). Female in dorsal view, approximately $\times 0.80$ (after Smith, 1887).

with granulated tubercles disposed as follows: one gastric, one genital, two cardiac, two on branchial ridge in line with lateral spine, and a tendency to rows of tubercles on branchial regions. Rostrum with a long, narrow, obtuse tooth with a denticle on each side, a subacute basal tooth, and below and outside this a short spine. Supraorbital spine blunt, postorbital spine smaller but somewhat sharper; upper side of emargination on eye spined.

Chelipeds long, rough, armed with laciniated teeth and spines on both margins; merus with an additional median row of spiniform tubercles on upper surface; carpus with largest spine at inner angle; hand with an obsolete median row beneath. Meri of walking legs spinulose, also carpus and propodus of last pair; dactyls furred; a tubercle on sternum at base of cheliped and each of legs one to three.

Abdomen with a large tubercle in middle of second to sixth abdominal segments and a conical tubercle at extremity of segments two and three; segments three to five fused in male. Lower surface of body granulate and tuberculate.

Measurements.—Carapace: male, length, 36 mm.; width, 47 mm. Length of cheliped, 122 mm. Carapace: ovigerous female, length, 11 mm.; width, 13 mm.

Variations.—The species varies greatly in the number and prominence of tubercles and teeth, and in constriction and ornamentation of the rostrum. The elevations of the carapace may bear spines or tubercles.

Color.—Purplish red with cross bands of buff on chelipeds and walking legs; palms pinkish brown (various authors).

Habitat.—The species is found predominantly on sand or sandy mud bottoms (Rathbun, 1925); 10 to 134 fathoms.

Type localities.—Off Conch Reef, French Reef, and American Shoal [southern Florida].

Known range.—Off Marthas Vineyard, Mass.; latitude of New Jersey through West Indies to Grenada.

Remarks.—Ovigerous females are known from North Carolina in December.

Parthenope (Platylambrus) fraterculus (Stimpson)

Figures 249, 252D

Lambrus fraterculus Stimpson, 1871a, p. 130.

Parthenope fraterculus: Rathbun, 1925, p. 525, pls. 186–187; pl. 190, fig. 2 (rev.).

Recognition characters.—Carapace subtriangular, approximately four sided, posterolateral margins continuous with sides of posterior margin, and long anterolateral margins in line with rostral borders. Depressions separating branchial from cardiac and hepatic regions deep; cardiac



FIGURE 249.—*Parthenope (Platylambrus) fraterculus* (Stimpson). Male in dorsal view, position of legs reconstructed, legs of left side not shown, 5 mm. indicated.

and gastric regions connected by a narrow ridge, hepatic and branchial regions by a wider ridge bounded below by a deep hollow visible in side view; hepatic region with a large submarginal tubercle visible in dorsal view. Margin of branchial region cut into 11 to 13 small teeth; posterior margin with 3 equal teeth. Prominences of carapace ornamented with a few large tubercles and spines as follows: three gastric in a triangle, one genital, two cardiac, and three on branchial ridge. Front inclined about 45 degrees, ending in a narrow, blunt tooth, a blunt tooth on each side above antennules, and outside, below these, a small slender spine. A tubercle on preorbital lobe; orbit with a small blunt tooth on inner lower angle and a large tubercle between this and angle of buccal cavity. Endognath with row of five tubercles near outer margin.

Chelipeds of male approximately 2.5 times as long as carapace; inner, outer, and upper margins of merus with a few unequal stout spines; inner and outer margin of hand armed with triangular, denticulate, unequal teeth, six or seven larger ones on inner, three or four on outer margin; largest tubercle on upper surface at proximal third conical. Walking legs with meri denticulate; dactyls furred except at tip; carpus and propodus of last pair with two or three lobes above and five denticles below.

Sternum and abdomen tuberculate, second to sixth abdominal segment with a large transverse tubercle.

Measurements.—Carapace: male, length, 16 mm., width, 17 mm.; female, length, 16 mm., width, 18 mm.

Variations.—There is great individual variation in the nature of tubercles and spines. In some individuals the prominences are low and blunt, in others high and sharp. The front may vary in degree of inclination, and margins of the frontal lobes and orbits may be denticulate, entire or subentire.

Color.—Uniform red, eggs bright red (various authors).

Habitat.—The species has been taken predominantly on rocky or shelly bottoms (Rathbun, 1925; Holthuis, 1959); 4 to 110 fathoms.

Type localities.—Off Sand Key, Carysfort and Conch Reefs, West of Tortugas, 26 to 68 fathoms [southern Florida].

Known range.—Off Cape Fear, N.C.; Gulf of Mexico, off Cape San Blas, Fla., to Florida Straits; off Cape Catoche, Yucatan, Mexico; through West Indies to mouth of Amazon River (U.S. National Museum records).

Remarks.—Ovigerous females have been reported in May from southern Florida (Rathbun, 1925), and August from northeastern Florida (U.S. National Museum records).

Genus *Solenolambrus* Stimpson, 1871

Garth, 1958, p. 458.

Solenolambrus tenellus Stimpson

Figure 250

Solenolambrus tenellus Stimpson, 1871a, p. 134.—Hay and Shore, 1918, p. 463, pl. 39, fig. 8.—Rathbun, 1925, p. 541, pl. 194, figs. 3–4; pl. 279, figs. 5–9 (rev.).

Recognition characters.—Small delicate species. Carapace but little broader than long and about equally produced in front of and behind line of lateral angles; surface punctate; protuberances of gastric and cardiac regions fairly well marked near posterolateral margin but almost obsolete anteriorly. Anterolateral margins of carapace crenulated, five or six teeth on expanded and broadly rounded lateral angle being most prominent and defined chiefly by impressed lines on marginal shelf; hepatic region with two or three denticulate teeth. Posterolateral margin concave; posterior margin convex, its lateral angles obtuse.



FIGURE 250.—*Solenolambrus tenellus* Stimpson. Female in dorsal view, walking legs of left side not shown, 3 mm. indicated.

Rostrum rather prominent, faintly tridentate at extremity, median tooth smallest and most prominent. External angle of orbit not prominent; eyes large with extremely minute tubercle at summit. Basal article of antenna approximately as long as next article. External maxilliped with ischium somewhat tuberculate near outer margin and extremity.

Chelipeds long, slender, general surface smooth, polished; edges denticulate. Merus with about 13 teeth on either edge, third tooth from distal end larger than others. Hand with 12 sharp forward-curving teeth on superior edge, terminal tooth above finger spiniform and considerably longer than others; outer margin with about 11 small teeth, inner with 19 or 20 minute teeth. Walking legs naked, compressed, without lamini-form crests; merus of last pair slightly expanded below near base.

Abdomen and sternum of male coarsely pitted, otherwise smooth and glabrous.

Measurements.—Carapace: male, length, 6 mm.; width, 6 mm. Length of cheliped, 16 mm. Carapace: ovigerous female, length, 5 mm.; width, 6 mm.

Habitat.—Thirty to 115 fathoms.

Type localities.—Off Carysfort, Conch, and French Reefs, 35 to 49 fathoms [southern Florida].

Known range.—Off Cape Lookout, N.C.; Gulf of Mexico, near Cape St. George, Fla., to Florida Keys; Bahamas; Barbados.

Remarks.—Ovigerous females have been reported in May from Barbados, May and June from Florida (Rathbun, 1925), and questionably in August from North Carolina (an incompletely labeled specimen from Hay and Shore's material in Institute of Fisheries Research collection, and *Fish Hawk* records for 1902).

Genus *Heterocrypta* Stimpson, 1871

Garth, 1958, p. 473.

Heterocrypta granulata (Gibbes). Pentagon crab

Figures 251, 252E

Cryptopodia granulata Gibbes, 1850, p. 173.

Heterocrypta granulata: Hay and Shore, 1918, p. 464, pl. 39, fig. 9.—Rathbun, 1925, p. 555, text-fig. 152, pl. 203, figs. 1–2; pl. 282, figs. 1–3 (rev.).

Recognition characters.—Carapace subtriangular, with wide clypeiform vaulted expansions, length two-thirds width; general surface smooth,



FIGURE 251.—*Heterocrypta granulata* (Gibbes). Male in dorsal view, 10 mm. indicated.

punctate; margins crenulate. Anterolateral margin nearly straight, with dorsal surface sloping upward from margin to prominent, granulate branchial ridge running parallel with each side, these connected by a short transverse ridge on

gastric region and joined behind to posterior marginal ridge. Rostrum broad, blunt, deflexed, with rounded margins connected to gastric ridge by a pair of granulate crests. Orbits small, nearly circular; eyes small, retractile. Cardiac region with a large domelike elevation granulated at summit.

Chelipeds unequal, rather heavy, longer than width of carapace; outer and inner margins of upper surface of merus, carpus, and hand expanded into irregular granulate or dentate crests; fingers short, agape in larger cheliped. Walking legs short, almost completely hidden beneath carapace.

Sternum and lower surface of abdomen coarsely granulate; male abdomen with third, fourth, and fifth segments fused, sixth segment with a sharp proximal appressed spine with tip lying between two tubercles on fifth segment.

Measurements.—Carapace: male, length, 12 mm., width, 18 mm.; female, length, 15 mm., width, 21 mm.



FIGURE 252.—Family Parthenopidae, first and second right pleopods of males; A, *Parthenope agona* (Stimpson), medial view; B, *Parthenope serrata* (H. Milne Edwards), medial view; C, *Parthenope pourtalesii* (Stimpson), medial view; D, *Parthenope fraterculus* (Stimpson), medial view; E, *Heterocrypta granulata* (Gibbes), medio-sternal view; 1 mm. indicated.

Color.—Varying from light gray to nearly black, usually commingled so as to produce an irregular mottling or marbling (various authors).

Habitat.—This species is found on shingly bottoms, and not infrequently on shelly bottoms in Morehead City, N.C., harbor. Its angular form and coloration bear so close a resemblance to fragments of shells among which it lives that it is extremely difficult to detect. Two to 75 fathoms.

Type localities.—Near Kiawah Island, Sullivan's Island, and White Point Shoal, Charleston Harbor, S.C.

Known range.—Nantucket Sound, Mass., to Georgia; Florida Straits to Sabine, Tex.; through West Indies to St. Thomas.

Remarks.—Ovigerous females are found in the Beaufort, N.C., area throughout the summer.

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